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PHILOSOPHICAL TRANSACTIONS.

I. *On the Organization of the Fossil Plants of the Coal-measures.*—Part VII. Myelopteris, Psaronius, *and* Kaloxylon. *By* W. C. Williamson, *F.R.S., Professor of Natural History in the Owens College, Manchester.*

Received June 3,—Read June 10, 1875.

The existence or non-existence of the remains of Palms in the Carboniferous strata has long been a debated geological question. Accepting the determinations of Corda as announced in his 'Flora der Vorwelt,' many geologists admitted these true endogens into their lists of Carboniferous plants. Cotta had figured, in his 'Dendrolithen,' three very anomalous stems, under the names of *Medullosa porosa*, *stellata*, and *elegans*. Corda, in his 'Flora der Vorwelt,' subsequently figured two stems from Carboniferous strata obviously allied to one, at least, of Cotta's types, under the names of *Palmacites carbonigerus* and *P. leptoxylon*, which he placed in the class of Palms. Cotta's figures of *Medullosa elegans* are very misleading, though they are not very unlike the specimens which he probably described. Some specimens now in the British Museum which came direct from Cotta, and for having my attention drawn to which I am indebted to my friend Mr. Carruthers, exhibit a remarkable areolation when cut transversely. This areolation Cotta has not only copied but exaggerated; hence the peculiar aspects of his figures 1 & 8 of his *Medullosa elegans*; it certainly is not a constant and normal feature, but the result of some change produced subsequent to the life of the plant—most probably a consequence of partial desiccation of the stem. Cotta's drawings of the cortical layer also are very misleading; hence it is very unsafe to accept his delineations apart from the study of his specimens, some of which, I fear, are no longer to be found. The consequence is that two of his species, *M. stellata* and *M. porosa*, remain too obscure to be relied upon without further evidence than Cotta has handed down to us.

The first to throw doubt upon the Monocotyledonous character of these plants was M. Brongniart in his 'Tableau des genres de Végétaux fossiles,' published in 1849, extracted from the 'Dictionnaire Universel d'Histoire Naturelle.' He identified Cotta's *Medullosa elegans* with some important plants not uncommon in the Carboniferous beds

of Autun; and whilst he thought that these specimens displayed a structure analogous to that of some Monocotyledons, especially of *Dracæna*, he adds, "il y ait des différences fort essentielles et qui rendent très-difficile d'établir des rapports entre ces fossiles et les végétaux vivants"*. M. Brongniart consequently proposed to make Cotta's *Medullosa elegans* the type of a distinct genus under the name of *Myeloxylon*. At a later page of his work (p. 97) he further gives a list of fourteen Carboniferous Monocotyledons, in which he includes seven species of *Trigonocarpum*, his proposed genus *Myeloxylon*, and the *Palmacites carbonigerus* and *leptoxylon* of Corda, at the same time declaring that all these supposed Carboniferous Monocotyledons are "très-douteuses et imparfaitement connues." At p. 89 of his work he retains Corda's genus *Palmacites*, but remarks respecting the two species from the Carboniferous strata, viz. *P. carbonigerus* and *leptoxylon*, that they appear to be distinct from the Palms, and probably also from the group of Monocotyledons, thinking them analogous to the *Medullosa elegans* of Cotta, adding, in reference to the latter plant, "qui n'est certainement pas un palmier."

In 1864 Goeppert referred to the *Medullosa elegans* under the name of *Stenzelia elegans*, separating it from Cotta's other species†, and regarding it as a generalized type of vegetable organization combining characters which are to be found separated in *Dracæna*, in Ferns, and in some Gymnospermous stems.

In January 1872 Mr. Binney made a very brief reference to *Medullosa elegans* in a communication to the Literary and Philosophical Society of Manchester, in which he says that "from some specimens in his cabinet he is led to believe that Cotta's *Medullosa elegans* is merely the rachis of a Fern or a plant allied to one"‡. The context shows that Mr. Binney had obtained specimens of the plant from the Carboniferous strata of Oldham.

In September 1873 I made a communication to the Botanical Section of the British Association for the Advancement of Science at their Meeting at Bradford, where I directed special attention to the organization of this plant, and announced my conviction that it was not only a Fern, but that it belonged to the aberrant group of the Marattiaceæ.

On January 26, 1874, my indefatigable fellow-labourer in the field of palæophytology, Professor Renault, presented to the Académie des Sciences of Paris another of his very important series of memoirs, entitled "Recherches sur les végétaux silicifiés d'Autun;" this last of which he designates "Étude du genre *Myelopteris*." Under this generic name he comprehends the *Medullosa elegans*, with its various synonyms of *Medullosa*, *Stenzelia*, and *Myeloxylon*. He assigns his reason for adopting the new name in the abstract of his memoir (which alone has yet been published) in the 'Comptes Rendus' of the above date:—"Pour conserver le nom, premier en date, donné par M. Brongniart à ces portions de plantes, et en même temps pour rappeler leur nature, je les désignerai sous le nom de *Myelopteris*." The reason thus assigned may probably suffice to justify

* *Loc. cit.* p. 60.

† Die fossile Flora der permischen Formation.

‡ Proceedings of the Lit. and Phil. Soc. Manchester, vol. xi. no. 7, p. 69.

me in following M. Renault's example, assuming the desirableness of abandoning Corda's name of *Palmacites* as misleading in this instance, and Cotta's term *Medullosa* as belonging to the other species of his genus.

Examples of very young or terminal rachides of *Myelopteris* are not uncommon, since Mr. Butterworth and the late Mr. Whittaker have added specimens of such to those which I have collected myself. More matured petioles are much more rare. In addition to two or three which I have met with, I have received one very fine section from Mr. Butterworth, and Captain J. Aitken, of Bacup, has placed in my hands an interesting example; but none of these rival in magnitude the examples from Chemnitz and Autun. M. Renault has kindly supplied me with a beautiful specimen from the latter locality.

Fig. 1 represents a transverse section of a petiole, for which I am indebted to Mr. Butterworth. The section is half an inch in diameter in one direction and $\frac{5}{16}$ in the other. It consists of a mass of parenchyma (*a*), the cells of which vary in diameter from ·006 to others of very much smaller dimensions, encased in a cortical investment (*b*), whilst scattered over the section are numerous gum-canals (*c*) and vascular bundles (*d*). The figure represents this section enlarged ten diameters. Though I have no longitudinal section of this individual example, I have such sections of similar ones which must be studied along with it. Fig. 2 represents a longitudinal section of the central part of a similar specimen to fig. 1, but enlarged 20 diameters. From this latter section we find that the cells of the medullary parenchyma (*a*) are arranged in more or less vertical lines, as is usually the case amongst Ferns, though, as seen in the figure, they are subject to much variation in this respect: this vertical arrangement is due to the tendency of the parallel walls of the cells to arrange themselves at right angles to the long axis of the petiole, a condition well shown in fig. 8.

Figs. 3, 4 & 4* represent three very young, or rather, perhaps, they may be termed terminal portions of the branched rachis. At the first glance these sections appear altogether different from fig. 1; but the differences are but apparent, since an unbroken series of links connects the two conditions, and shows that fig. 1 is but a more developed condition of fig. 3. Fig. 5 is a longitudinal section of a yet smaller rachis of the same kind as figs. 3 & 4, but giving off lateral branches (*h*), which are probably the petioles of leaflets. This figure is enlarged 16 diameters, the original specimen being little more than ·06 in diameter.

In the size and arrangement of their parenchymatous cells these several examples vary but little from what I have just described. In the young or smaller branches of the rachis (figs. 3 & 4), the most conspicuous objects are longitudinal canals, which appear in the transverse sections as large circular openings, varying ordinarily *in these young specimens* from ·005 to ·007 in diameter. The interior of these canals is frequently occupied by a slender column of pure coal, as in fig. 4, *c'*. The longitudinal section (fig. 2) exhibits these canals as running parallel with the long axis of the rachis, and having a nearly uniform diameter throughout their entire length. I have not been able

to detect any true walls enclosing them. They appear to be intercellular spaces, and to have served as gum-canals. In one longitudinal section only (fig. 6), in which a very small example of one of these canals accompanies a vascular bundle, the whole being magnified 65 diameters, the canal (*c*) appears as if it had originated in a row of enormously enlarged and attenuated fusiform cells which overlap each other at their oblique extremities. Since this is the only example of the kind which I have met with, I will not venture to affirm that all the canals have originated in the same way. In the young twigs these canals have a diameter varying from ·016 to ·004, being usually much larger than in the more matured petiole (fig. 1), in which they rarely exceed ·01 in diameter. In another very fine example of a matured rachis, for which I am indebted to Captain JOHN AITKEN, of Bacup, they are very much smaller (fig. 7, *c*), their diameter ranging between ·004 and ·0025. In another somewhat matured rachis, a portion of a transverse section of which is represented in fig. 9, the canals (fig. 9, *c*) are about ·007 to ·004, approximating to the diameter of those of the young twigs (figs. 3 & 4). It thus appears that these canals vary in their dimensions in different specimens; but I cannot discover any indication that such variations have any specific value.

The vascular bundles may next be examined. These vary both in different specimens and to some extent in different parts of the same specimen. In fig. 1 we can readily discern that these bundles are so arranged as to form a certain pattern or design. There is obviously a peripheral ring of them indicated by the letters *d*, whilst others occupying the more central parts of the section appear less regularly arranged; nevertheless a second irregular circular series may be traced, reminding us of what exists in certain recent ferns to which I shall call attention. This disposition to form a pattern is a feature that does not occur in endogenous plants. Each bundle consists of a cluster of vessels of various sizes, as seen in figs. 11 & 14, which represent two of the bundles of fig. 1. In fig. 11, for instance, the vessels (*d'*) are compressed and somewhat deranged in position, and are in close association with an enlarged gum-canal (*c'*), the entire cluster, including the canal, being invested by an imperfect sheath (*e*) formed of small cells. In fig. 11 we have one (*d*) of the smaller peripheral clusters, containing but three or four vessels (*d*).

The Vessels.—Fig. 7 represents a fine cluster of these as seen in a transverse section made from Captain AITKEN'S specimen. In this example the larger vessels (*d*) compress each other so slightly that they retain much of their cylindrical form, the intervals between them being occupied by small cells. The largest of these vessels has a diameter of about ·01, and the smallest of about ·0012. The larger vessels are always aggregated on one side of the bundle, and the smaller ones (*d'*) are clustered together much more compactly on its opposite side. Fig. 9, *d* represents part of a section with two bundles from another specimen in which the vessels are much fewer in number, and the very small ones seen at fig. 7, *d'* are almost wholly wanting. In some instances I don't find more than two or three large vessels and one or two small ones. In the young rachides (figs. 3, 4, & 4*) it is almost impossible to discover these bundles in the transverse

sections, since the vessels thus transversely divided closely resemble the parenchymatous cells, both in size and form; but on turning to such longitudinal sections of similar specimens as are represented in figs. 2–5 & 6, we see that they are abundantly present; but the largest vessels in such specimens do not exceed ·0025 in diameter. The number of vessels in each such bundle is also smaller than in the larger petioles. It is thus evident that the vessels in a bundle increase in number; and as they do so, either some of them increase in size, or those added at the later period expand into larger dimensions than was the case with those first developed. Fig. 4* is a transverse section of one of the smallest of these petioles that I have yet met with. On comparing its general form with that of the terminal rachides of *Angiopteris erecta* and other ferns, the projecting angles seen at the lower right and left margins of the fossil section, separated from the rounded central ridge by two deep flanking grooves, are seen to correspond exactly with those parts of the recent rachides which actually bear the leaflets. Hence I think I can scarcely be wrong in concluding that fig. 4* at all events is a section belonging to the terminal leaf-bearing portion of the petiole to which it belonged. It exhibits two very distinct gum-canals at *c*, *c*; the several larger openings nearer the centre of the section appear to have been similar canals which have become enlarged by some contraction of the surrounding parenchyma, as was probably the case with figs. 3 and 4.

On turning to vertical sections of these petioles, we discover that nearly all the vessels are either of the barred or of the spiral type. The large ones are chiefly of the former class, the spirals being mainly found amongst the smaller ones. Fig. 8 represents a longitudinal section of a bundle from the same specimen as the transverse section (fig. 7). The largest vessels are here seen at *d*, yet smaller ones at *d'*, and others still smaller at *d''*. Fig. 12 represents a single spiral vessel from the same section as fig. 7. The spiral is here formed not by one continuous thread, as in most Exogens, but by at least four parallel ones, as is so common amongst Palms. Carefully prepared sections of vessels like fig. 12 demonstrate that these are not modifications of reticulated tissue, but true spirals, since the threads of lignine seen crossing each other are shown by such sections to belong to the opposite walls of the vessels. In Captain Aitken's plant I found a very few unmistakably reticulated vessels. I have already mentioned the fact that these vascular bundles are aggregated with varying degrees of compactness. In fig. 7 a considerable quantity of cellular tissue is interposed between the larger vessels; and on turning to fig. 8, *a'* we see two of these sets of intervascular cells, each of which consists of three or four vertical rows of rectangular cells having a diameter of from ·002 to ·0006. Occasionally these cells are almost cubical, but they are usually elongated in the direction parallel with the vessels between which they are interposed. At figs. 8, *e* & 10, *e* we find a similar series of cells constituting an imperfect sheath to the vascular bundle. In the transverse section this sheath is often either absent or at least imperfect. In fig. 13 we have portions of two of the large vessels (*d*) of a vascular bundle from Captain Aitken's specimen with part of its investing sheath at *e*, *e*. The cells of the latter graduate rapidly into the ordinary interfascicular parenchyma.

The same appearance is observable in fig. 14, where, at *e*, we find a similar sheath. This latter bundle belongs to the specimen fig. 1. In some few instances I find a few prosenchymatous fibres entering into the composition of the sheath; but this is far from being a constant feature.

I have already described the numerous isolated gum-canals which enter into the structure of these petioles; but besides these we have numerous others associated with the vascular bundles. In the section (fig. 1) it will be seen that every one of the vascular bundles has connected with it a large round or semilunar orifice. In the enlarged fig. 14 one of these orifices (*c'*) is clearly seen to be enclosed within the cellular bundle sheath *e*. At first I was convinced that each of these was a large gum-canal which formed part of the bundle. Fig. 9 represents a small portion of one of several sections which I made of one specimen, in which very few bundles exhibit any trace of similar canals closely associated with the bundles, though such canals exist independently (fig. 9, *c*) in large numbers and of conspicuous size. On dissecting Captain AITKEN'S specimen, I found that many of its bundles were as devoid of open spaces as fig. 9. Others had semilunar lacunæ like those of fig. 1, whilst others were so exceedingly large and irregular as to form a cavity entirely surrounding the vascular bundle. One of these irregular orifices is seen in fig. 7, *c'*, *c'*; and on comparing it with the small gum-canals (*c*, *c*) in the same figure it becomes obvious that they are different structures. These and other similar facts led me to distrust my first conclusions, and made it probable that these open passages were rather spaces caused by the detachment of the vascular bundles from the surrounding cellular tissue, such as we frequently observe in sections of the recent Lycopods. Further studies of these sections led me to conclude that the explanation may be found in a combination of these hypotheses. Thus in fig. 8, *c* we have an unmistakable gum-canal associated with the large bundle represented there. In fig. 5, *c* similar combinations exist. In fig. 10, on the other hand, which is a longitudinal section of one of the bundles belonging to the same specimen as fig. 8, we have no gum-canal. Yet, as I have already shown, we cannot for a moment believe fig. 7, *c'* to represent, in any sense, the small canals (*c*, *c*) of the same figure. I conclude, therefore, that such canals are wholly absent from some bundles as in fig. 9; that they are distinctly present, but of small size, in such bundles as fig. 8, *c*; that they exist in similar position, but of much larger dimensions, in such cases as figs. 1, 2–6, & 14; and that in examples like fig. 7, such a canal, devoid of any true walls (being, in fact, a mere intercellular space), has constituted a weak point, which has been converted into a larger irregular cavity by the shrinkage of the neighbouring cellular tissues*.

There yet remains to be considered the cortical layer of this curious plant. Here again we meet with variations in different specimens. In very young rachides, like

* Since writing the above I have dried thin sections of the recent petioles of *Angiopteris erecta* between two plates of glass, and found that lacunæ were formed contiguous to each vascular bundle exactly corresponding with those seen in my fossils. This observation puts the origin of these large lacunæ in mechanical shrinking of the parenchyma surrounding the vascular bundles beyond the reach of doubt.—June 1st, 1876.

figs. 3 & 4, we find little more in each transverse section than a thin layer of a tissue (*b*) which is much more dense and opaque than the parenchyma which it encloses. Its inner margin is irregular. Longitudinal sections, like fig. 5, indicate that this tissue consists of compact prosenchyma, though in these specimens the mineralized condition is not favourable to the display of the details of its structure. In tangential sections of somewhat larger rachides we see this prosenchyma (*b*) is grouped in longitudinally disposed bands (fig. 15, *b*), which subdivide and again coalesce with each other at irregular intervals. These prosenchymatous cells appear to be slightly thickened by internal deposits, and have a diameter of from ·00125 to ·00062. In the above section the spaces between the prosenchymatous bands are occupied by prolongations of the medullary parenchyma (*a*). In the specimen, fig. 1, these fibrous bands are arranged in the transverse section as a series of small wedges, the contiguous bases of which form the outer boundary of the section, whilst their narrowed inner angles are separated by corresponding but inverted wedge-shaped prolongations of the medullary parenchyma. This arrangement is clearly shown by fig. 16, which represents a small portion of the cortical layer of fig. 1, further enlarged to 80 diameters. The coalesced bases of the prosenchymatous wedges are seen at *b*, *b*, and the outward prolongations of the medullary parenchyma (*a*) are seen at *a'*, *a'*. Since this section is made from a petiole that was wholly detached from the outer matrix, I cannot be sure that it exhibits the entire peripheral portion of the cortical tissues. But whether it does so or not it will be noticed that the fibrous wedges are arranged with considerable regularity in one linear series, and that no detached prosenchymatous bundles exist within that linear series. On turning to fig. 17, which represents a similar section to the last, but taken from Captain AITKEN'S specimen, we see that we not only have, at *b*, the wedges similar to those in fig. 16, but in addition we have an inner series of detached rounded or elliptical bundles at *b'*, *b'*, and a further set of crescentic ones at *b''*, *b''*, the latter being in contact with the large gum-canals (*c*, *c'*) which abound in the cortical portion of the section. In the section (fig. 16) the cortical layer has a thickness, measuring from the base to the apex of each wedge, of about ·016. The area occupied by the prosenchymatous bundles in fig. 17, amounting to ·03, including the detached ones, will sometimes be rather greater than in fig. 16. In the specimens described thus far I find no definite trace of any layer external to the prosenchymatous one; but I have some examples in which I find clear evidence that in them the parenchymatous tissues are prolonged beyond the prosenchymatous ones, and appear to constitute a yet more peripheral layer of parenchyma. This is very clearly shown in sections made from the same specimen as that of which fig. 17 represents a portion. When this is the case the whole of the prosenchymatous bundles become enclosed in parenchyma, and converted into more or less completely detached hypodermic islets. This condition is somewhat important to us when we endeavour to ascertain the homologies of these structures in relation to living Ferns.

Similar prosenchymatous bundles to those just described, but of smaller size, occur

in some of my specimens in the more central parts of the rachis. I have already mentioned that a few fibres occasionally unite with the small parenchymatous cells to compose the imperfect sheath of the vascular bundles. But besides these we find free bundles, occasionally in contact with a gum-canal. At other times I discover one or two such outside, but not far removed from the sheaths of the vascular bundles. Fig. 13 represents one of these bundles enlarged 350 diameters; *d*, *d* are portions of two of the vessels belonging to a large vascular bundle, of which, as we have already seen, *e*, *e* is the cellular sheath and *g* is the prosenchymatous bundle composed of thickened fibres and imbedded in the medullary parenchyma. In the specimen figured a second bundle existed in similar relationship to the vascular bundle *d d*.

There yet remains to be considered the branching of these petioles. In fig. 5, which in all probability represents one of the ultimate subdivisions of the true rachis, we have a distinct branchlet given off at *h*. From its size I imagine this must have been the small petiole of a leaflet; a second and similar one is obviously being given off at *h'*. If these are, as I suppose, the ultimate petioles of leaflets, the latter have been arranged in this specimen, at least, at intervals of about half an inch apart. In another of my examples a rachis of about a quarter of an inch in diameter is giving off a lateral branch of about an eighth of an inch in diameter. In both these cases the secondary branches are given off at right angles to the primary one, and not obliquely, corresponding in this respect to their arrangement in the *Myelopteris Landriotti* of M. Renault*.

In fig. 1 a large cylinder of cellular tissue, with a vascular bundle within it but pushed out of its normal central position, is seen at *x*. This is a small rootlet of *Stigmaria* which, as is so often the case, has forced its way into the ruptured interior of the petiole.

These descriptions will, I think, make it plain to the experienced student of vegetable organography that the subject of them cannot be a Palmaceous Monocotyledonous plant. The structure of the vascular bundle, especially the restriction of its vascular tissue to spiral and barred forms, with the absence of all traces of phlœm-structures, makes this sufficiently obvious. In like manner, though at first sight its remarkable layer of hypodermal woody prosenchyma bears a superficial glance to the peripheral fibre-bundles of a palm, yet their structure and arrangement are very different in the two cases. It was the peculiarities displayed by these two tissues that led me to seek for the true affinities of those plants amongst the Marattiaceæ, their close resemblance to which, as I have already mentioned, I demonstrated at the Meeting of the British Association for the Advancement of Science in September 1873. My friend Professor Renault announced that he had arrived at the same conclusion, after studying the Autun examples of this type, in his memoir presented to the Academy of Sciences at Paris in January 1874. At that time we had not exchanged our views on the subject; hence our united, but independent, testimonies render our joint conclusion an exceedingly probable one. I may observe that there is no doubt that the Autun plants corre-

* Comptes Rendus, 26 Janvier 1874.

spond very closely with mine from the Oldham Upper foot-coal and Ganister-bed. The principal difference between the French and English examples that I have seen is in their size, some of the former being nearly four times the diameter of the largest of those which I have obtained from our older coal-fields. I am indebted to M. Renault for a beautiful specimen from Autun which is fully two inches in diameter. I have, as yet, met with nothing like this in our Lancashire beds; but it corresponds closely enough with the dimensions of the swollen bases of the petioles of *Angiopteris erecta* and others of the larger Marattiaceæ. M. Renault finds the gum-canals in his specimens more numerous in the centre of the petiole than at its circumference. In mine these canals are pretty equally distributed over the entire transverse section. Such canals are found abundantly in most of, if not all, the Marattiaceæ, though they are not confined to this aberrant type of the Ferns. I find them very well represented in the petioles of *Cibotum princeps*.

In the petioles of *Marattia fraxinea* and *M. laxa* these canals are of large size, but chiefly found in the medullary parenchyma, especially in its more central portions, being wholly absent from the hypodermal prosenchyma.

On the other hand, in *Angiopteris Teismaniana*, *A. erecta*, and *Marattia ascensionis*, they not only exist in the parenchymatous portions, but they are equally abundant, though of smaller size, in the dense layer of sclerenchyma* which encases the inner parenchyma. In several of my figures of the fossil forms I have represented these canals as being more or less filled with a cylindrical rod of black carbon, as in the example of fig. 17, *c'*. I have seen nothing like this in any of the vascular tubes, whilst in the canals it is the common condition. It appears to me that this difference is due to something more than mere infiltration of carbonaceous matter in the case of the intercellular canals; in all probability the black substance is the carbonized residuum of the gum with which these canals were once filled.

M. Renault has already called attention (*loc. cit.*) to the fact that whilst in our fossil examples the hypodermal sclerenchyma forms an interrupted layer, in the recent Marattiaceæ it forms a continuous one. The inner margin of my sections of *Angiopteris erecta* display an irregular dentate outline, which approaches in some slight degree to that of fig. 1. M. Renault has further pointed out that ordinarily in *Angiopteris* there are isolated bundles of sclerenchyma within and detached from the continuous hypodermic layer. As already shown, I find these islets to be wanting in *Marattia laxa* and *M. fraxinea* (that is, in the two species which exhibit no gum-canals in the sclerodermic layer), whilst they are present in *Angiopteris Teismaniana*, *A. erecta*, and *Marattia ascensionis*; they are also more conspicuous in the thick bases of the petioles than in their slender upper extremities.

The differences in the thickness of the sclerenchymatous layer in my specimens

* I have used this word, not in the limited sense in which it is employed by Meitenius, but in the broader one suggested by Sachs in his 'Lehrbuch der Botanik,' 2nd edition, p. 76, where he proposes the application of the term to all hardened prosenchymatous as well as parenchymatous cells.

figured is probably due to age, since I find that in *Angiopteris erecta* this layer is scarcely visible in the ultimate leaflet-petioles, but is from ·004 to ·008 in the secondary rachis. In the upper portions of the primary rachis, where the latter has a diameter of about three eighths of an inch, this layer has a thickness of about ·016, whilst near the base of the same petiole, where the latter has a diameter of nearly 2 inches, the sclerenchyma is nearly ·05 in thickness. Similar conditions appear to have prevailed in our fossil forms.

In all the recent examples of Marattiaceous Ferns we have a very distinct ring of parenchyma external to the sclerenchymatous cylinder; which parenchyma is often more or less completely separated into three layers by the development in its more central cells of a quantity of chlorophyl. This superficial parenchyma is very distinct in all the species which I have examined, but is the least developed in *Marattia fraxinea*. I have called attention to the existence of indications of a similar layer external to the sclerenchyma of some of my fossil examples; but these specimens have not enabled me to detect the epidermal layer, with its stomata-like openings, which Professor Renault has found in his well-preserved silicified fragments.

Whether or not all my fossil examples belong to the same species may be doubtful, since they exhibit considerable differences in the diameters of their gum-canals; but as many of these may, as in fig. 4*, have undergone some alteration in size owing to contraction of the parenchymatous cells, I think it unsafe, in the present state of our knowledge, to make these differences specific features. There are also differences in the structure of the sclerenchymatous hypoderm, as shown in figs. 16 & 17; but I cannot satisfy myself that these differences have more value than the variations in the canals.

The specimens next to be described also belong to the class of Ferns, and are interesting because they show that the fossils with which we have so long been familiar from the coal-fields of the continent under the general name of *Psaronites* are not absent from the Lower Coal-measures of Lancashire; but though the evidence I am about to advance clearly shows the correctness of the above statement, it must be confessed that our representatives of this group of objects present themselves in very humble guise contrasted with the magnificent examples of *Psaronius* and *Protopteris* figured in the pages of Corda's 'Flora der Vorwelt.'

The probable existence of tree ferns in the British Coal-measures was long ago pointed out by the late Professor Phillips, and by the authors of the 'Fossil Flora of Great Britain.' But these observers derived their conclusions solely from the external forms of certain stems. At the Meeting of the British Association for the Advancement of Science in 1872, Mr. Carruthers described what he believes to be eight forms additional to the two figured in the 'Fossil Flora' of Lindley and Hutton. All these examples appear to have been obtained from the Bath coal-field. Hence I believe that the specimens of this group which I am about to describe are the first that have been

met with in the coal-fields of Lancashire*. Some of them I have obtained myself. For others I am indebted to Mr. Butterworth; but for my best examples I had to thank the late Mr. J. Whittaker†.

With two exceptions my specimens are confined to small masses of the adventitious roots so characteristic of the *Psaronites* and arborescent Ferns; but in two instances I have obtained the outer layer of epidermal and subepidermal tissue from which the rootlets more immediately sprang. Fig. 18 represents a transverse section of one of these of the natural size; the outer or cortical parenchyma of another specimen with several rootlets passing downwards and outwards through it is enlarged 24 diameters in fig. 19. This cortical layer consists of a somewhat irregular parenchyma, composed of cells which are usually from about ·01 to ·006 in diameter. At the innermost portion of this cortex (fig. 19, *b*) the structure is somewhat confused; the regular parenchyma has interspersed through it a number of irregular cavities, each of which seems to have been either a large cell, or to have resulted from the rupture of two or three cells which have united to form a common cavity. As we proceed outwards, the cells (*b'*) become somewhat larger than at the inner portion of the cortex. At *i*, *i* we have several rootlets seen in transverse section, some of them being divided into two halves by an accidental fissure which has extended through this portion of the bark and been filled up with infiltrated crystalline carbonate of lime. At *b''* we find the parenchymatous cortical cells increasing still further in size, becoming lax in their aggregation, and finally being prolonged into a number of epidermal hairs such as frequently clothe the adventitious roots of living tree ferns—such, for example, as *Cyathea dealbata*.

Fig. 20 represents an enlarged portion of fig. 18, which latter is a cluster of adventitious rootlets free from the cortical parenchyma which encloses them in the case of fig. 19. Here the interspaces between the rootlets are seen to be occupied by numerous epidermal hairs. Fig. 21 is a portion of fig. 19 yet more highly magnified.

Each rootlet, when free from the cortical parenchyma, has a diameter of from ·075 to ·12. Externally it consists of a very well-defined cylinder of sclerenchymatous prosenchyma (figs. 20 & 21, *l*). This cylinder-wall is from ·012 to ·015 in thickness. The fibres of which it is composed have a diameter of from ·00125 to ·003. Within this cylinder there has doubtless been a mass of cellular tissue, which has disappeared in every instance that I have yet seen; but each rootlet retains more or less distinct traces of the central bundle of small vessels (fig. 20, *m*). Their state of mineralization prevents my determining their characters with absolute certainty; but some of the fragments indicate that

* Since this Memoir was read I find that fragments of tree ferns with aerial roots were figured and described by the Rev. Henry H. Higgins, M.A., "On some Fossil Ferns in the Ravenhead Collection, Free Public Museum, Liverpool," p. 3, pl. 11. figs. 2 & 3,—June 2nd, 1876.

† I much regret that since my last memoir was read I have to speak of this valuable auxiliary in the past tense. He was an excellent example of the scientific operative for which Lancashire has so long been celebrated. His zeal for the investigation of the plants of the Coal-measures was only equalled by the open-handed liberality with which he placed his valued treasures at the disposal of any one who was able and willing to use them for scientific purposes.

they belong, as might be expected, to the barred type. They are very distinctly preserved in a transverse section of one rootlet, in which the bundle consists of about a dozen vessels, of which the largest have a diameter of ·0025, whilst the smallest are not more than ·0008. This bundle is represented in fig. 22. The epidermal hairs (figs. 20 & 21, *k*) are extremely numerous and well defined; they are cylindrical, and composed of a single linear series of cells with rectangular transverse septa, which are often indistinctly seen. Their diameter averages ·0017. The length of the cells is variable, but those which I have measured are usually about ·015. Fig. 19, *b''* shows that these hairs are but extensions of the outermost interradicular parenchyma (*b'*).

In the absence of all trace of the more central and vascular portions of the main axis to which these adventitious rootlets have belonged, it is impossible to determine to what class of Ferns they belong*. In the form of the vascular bundle of the rootlet it

* As stated above, when my memoir was written I had found no trace of the vascular axis of the plant here described; but the day before this memoir was laid before the Royal Society Mr. Carruthers kindly showed me some sections of the plant from his cabinet, amongst which was one of which fig. 22* is a representation, of the size of nature. In the upper left-hand corner of this section there is preserved a small portion of a central stem. This part of the section is further enlarged ten diameters in fig. 22**, in which *d d* is a narrow lamina of vessels which appears in the transverse section as a semicircular band. These vessels are not arranged in any regular radiating order, and exhibit no trace whatever of having received any increase to their number from exogenous growths. The character of the vessels does not appear in the transverse section, and unfortunately no longitudinal one appears to have been made of the specimen. The vessels vary in size; but the greater number of them have a mean diameter of from ·0033 to ·005, some few being larger and others smaller than these dimensions. This vascular belt is interrupted in the middle; but whether this break is an accidental rupture, or whether the two halves represent parts of separate crescentic masses, is not certain. This vascular lamina has evidently been imbedded in a mass of very regular parenchyma, an inner portion appearing at *a*, whilst fragmentary portions remain of a peripheral mass which has occupied the interval between the vascular layer and the periphery of the stem from which the numerous rootlets (*i*) have sprung. The inner parenchyma (*a*) and the inner portion of the outer parenchyma correspond very closely, and consist chiefly of cells that have a diameter of from ·0025 to ·005. But the more peripheral portion of the outer tissue consists of a dense mass of very regular, small, thick-walled cells, with a diameter of from ·001 to ·0006, approximating closely in their appearance in the transverse section to the fibres constituting the outer layer of each rootlet. A curious feature of these parenchymatous structures is the presence in them of numerous longitudinal canals (*c, c*), which appear to be identical with the gum-canals of the *Myelopteris* described in the earlier part of this memoir.

Whether the stem originally contained a single circle of these vascular laminæ, or whether there were successive layers concentrically arranged, as in many species of *Psaronius* figured by Corda, is not determinable from Mr. Carruthers's sections. The great probability, however, is that the latter condition has existed. It will be observed that this, the only stem of a tree fern from the British Carboniferous deposits of which the internal organization has hitherto been described, exhibits the same absence of all exogenous growths as that to which I called attention in some of my previous memoirs as characterizing the continental *Psaronites*. So far as my present experience has extended, all the fossil ferns had, like their recent allies, closed vascular bundles; whilst the Calamites and Lycopods, including in the latter group the *Asterophyllites*, had open ones. If *Lyginodendron* and *Heterangium* ultimately prove to be stems or rhizomes of Ferns, of course this generalization will have to be discarded; but I have as yet obtained no such proof.

Mr. Carruthers's cabinet contains a beautiful section of *Myelopteris*, in which the outer vessels of each vascular bundle are small, but with unusually thick walls, as seen at *d'* in fig. 7*, which represents one of these bundles, with a small portion of the surrounding parenchyma, much enlarged.

approaches nearest to Corda's *Psaronius radiatus*; but it differs wholly from that plant in the cellular hairs with which its roots are clothed. The only plant which Corda has described in which the roots are similarly furnished is his *Protopteris Cottai*; but in that plant the sclerenchymatous cylinder of each root is invested by a thick composite layer of parenchymatous cells, whereas in my plant the hairs spring abruptly from the exterior of the sclerenchymatous cylinder. As this appears to be an undescribed species, I may be permitted to dedicate it to my friend Professor Renault, from whose labours amongst the fossil plants of Autun so much good has already arisen, and is likely yet further to arise. Our investigations, proceeding side by side, mutually illustrate each other, and will eventually afford the means of establishing some trustworthy comparisons of the flora of the French coal-field with that of Lancashire. I propose to designate my plant the *Psaronius Renaultii*. It is of course possible that it may some day be proved to be the base of a *Caulopteris*, or some other of the supposed tree ferns whose stems have already been discovered in the Coal-measures.

The next plant which I propose to describe is one of the most remarkable as well as the most beautiful of those which I have met with in our Lancashire deposits. On the first glance at its structure we might suppose the Carboniferous forests to have been hung with Bignoniaceous Lianos like those of Brazil; but closer examination demonstrates that this resemblance is only a superficial one. At the same time a remarkable instance is furnished by this plant of those resemblances between very different objects that have of late years attracted the attention of botanists. Figs. 23–26, 32, 33, 34, 37, and 38 show the vascular portions of the stem arranged usually in six, but, in the case of the two last-named figures, respectively in five and four wedges, separated by corresponding inward prolongations of the cortical tissues—a condition which forcibly reminds the botanist of similar transverse sections of the stems of Bignoniaceæ. But further examination shows that my fossils are very different from that recent type, since their central axis is, like that of some of the arborescent Lycopodiaceæ which I have already described, composed of a mass of vessels. This axis forms the nave-like centre from which the six large vascular wedges radiate like the spokes of a wheel, each of these primary wedges being separated by medullary rays into a multitude of secondary ones. The bark is differentiated into several distinct portions, and the whole structure is invested by the double row of vertically elongated cells indicated by the letter *k* in each of the figs. 23, 24, 25, 28, & 36. That the six radiating primary wedges are the products of exogenous growth is clearly shown by the sections of young twigs represented by figs. 24 & 25, in which specimens the central vascular axes alone exist—a condition of things reminding us strongly of what I have already described in the stems and twigs of *Asterophyllites*, and of some of the Lepidodendroid plants. I think there can be no doubt but that, as in the case of the triangular axial bundle of *Asterophyllites*, each of the hexagonal ones of figs. 24 & 25 represents the axial bundle of a young twig, and that the radiating vascular laminæ constituting the six primary wedges are the results of exogenous processes of growth, which have converted leafy twigs or branches into matured stems.

Each of the numerous specimens figured in this part of my memoir exhibits some morphological feature, important to be noted, in a better state of preservation than in the other examples. Hence, instead of describing each specimen separately, it will be convenient to examine successively the several structures constituting the plant, proceeding from within outwards. Since it appears easy to identify the homologies of this plant with those of *Lepidodendron* and *Asterophyllites*, I shall revert to the letters of reference employed in the memoirs describing those plants, to represent what appears to me to be identical or closely related structures in each of these three types of organization.

The central axis (*c*) in fig. 23 has a diameter of ·04. In figs. 32, 33, & 34 its diameter is ·024, the central tissues in these three sections having been destroyed. In fig. 26, which is a section from the same stem as the last three, but about half an inch higher up than fig. 34, it is rather larger; but it has been subjected to a little lateral compression, giving it an oval instead of a rounded outline. In fig. 25 it is ·028, and in fig. 24 it is ·024. In fig. 37 it is ·008, whilst in fig. 38 it only consists of a few vessels. The entire diameter of the stem in fig. 23 is about 0·1, whilst in figs. 32–34, had the bark been perfect, it would probably have been about 0·14.

So far as I can ascertain, this central axis consists wholly of a bundle of vessels, which vary in size. The more conspicuous, larger ones in fig. 23 vary from ·005 to ·0025; in fig. 37 the largest are not more than ·0012, whilst in the young twig (fig. 25) the largest of them average about ·0025. It thus appears that they increase in size with the age of the stem, judging of that age from the degree of development of the exogenous cylinder. I have not succeeded in obtaining proof of the existence of any cellular tissue mingled with these vessels; neither do they display any regularity in their arrangement; irregular clusters of the larger vessels are connected by smaller ones, as represented in figs. 23 & 26. Those occupying the periphery of the bundle are generally uniformly smaller than is the case with those of the more central portion. In the two young twigs (figs. 24, *c* & 25, *c*) the entire bundle has a distinct hexagonal transverse section; but this definite hexagonal contour is scarcely traceable in those examples which possess an exogenous zone. Longitudinal sections show that all the vessels of the central axis are, like those of the exogenous wedges, of the reticulated type (fig. 29, *e*). I have not yet discovered in any of my sections a single barred or spiral vessel.

The Exogenous Zone.—As already stated, this consists of from four to six separate primary wedge-shaped masses of vessels, each of which is composed of numerous laminæ in which the vessels are arranged in regular radiating series. In every one of what appear to be adult stems, such as figs. 23, 26, 32, 33, & 34 these wedges are six in number. The innermost vessels of each wedge are somewhat smaller than the more peripheral ones. In fig. 1 the largest peripheral vessels are about ·0025; in fig. 32 they are about ·0037; in fig. 37 the larger vessels are also about ·0025. The number of the radiating lines of vessels seen in a transverse section of each primary wedge varies even in the same plant. Still more so when we compare figs. 37 & 38 with those of the more matured stems. The number of vessels composing each radiating

series obviously varies with the age of the axis. Even in the transverse sections the existence of medullary rays is sufficiently obvious. In fig. 31, which represents a small portion of the periphery of one of the primary wedges of fig. 34, these medullary rays are clearly shown at *f*, where they appear as parenchymatous cells elongated radially. Fig. 30 is a tangential section of a stem intersecting three vascular wedges, the central one (*d*) having been cut through at its innermost portion close to the central vascular axis. In this section the medullary rays appear at *f f*, as clusters of cells arranged vertically as single linear series. In fig. 27 we have a tangential section of a similar wedge at its more peripheral extremity. These two sections combined illustrate the increase in diameter of the vessels composing each primary wedge as we proceed from within outwards; and fig. 27 further demonstrates a corresponding increase in the number and dimensions of the medullary rays (*f*). In the latter figure we find that many of these rays are lengthened vertically by a material increase in the number of their component cells; and, further, that from time to time we meet with portions of these rays, as at fig. 27, *f'*, in which two and even three vertical lines of cells coexist in the same ray. Fig. 29 represents a portion of a slightly oblique, radial, longitudinal section crossing two vascular laminæ (*e*, *e'*), with parts of the medullary ray (*f*) which separate them. The latter exhibits the usual mural arrangement of its cells seen in radial sections of so many others of the Carboniferous plants. In the tangential section (fig. 27) the vertical length of these cells ranges from ·001 to ·0025.

The Cortex.—This part of the organism exhibits some very characteristic features which distinguish the plant under consideration from any of those which I have hitherto described. The six large primary wedges of the vascular zone are separated by a mass of delicate thin-walled parenchyma. The arrangement of the cells of this structure is best shown in the two figures 26, *h* & 32, *h*. The cells are parenchymatous, but are elongated radially, showing a tendency to arrange themselves in lines more or less parallel with the sides of the two contiguous primary vascular wedges. On approaching the broad outer extremities of these wedges, the elongated cells exhibit a strong tendency to diverge in two groups, each one bending round the peripheral extremity of the woody wedge nearest to it, whilst in the angular space between and external to the diverging portions we have ordinary regular parenchyma. I do not mean to convey the impression that all these portions of the cellular tissue are separated by clearly defined boundaries; such is not the case; but whilst these respective areas graduate into each other, there is little difficulty in tracing broadly their respective characteristic features, which are well shown in fig. 34, *i''*. The same figure further shows, at *g*, *g*, another remarkable feature; the cellular masses (*h*) do not bend round the outer extremities of the primary wedges (*d*, *d*) as just described, in immediate contact with those wedges; but they enclose a small semilunar area (*g*) coextensive with the diameter of the wedge, and which is occupied by a distinct form of cellular tissue. I shall shortly give my reasons for believing that this latter tissue is a quasi-cambial meristem layer, which is concerned in the formation of the newest exogenous vascular growths. The general features of

the cells of this meristem tissue are shown in fig. 31, *g*. The outer extremities of all the medullary rays terminate in it; and as they do so those of opposite sides of each primary wedge bend inwards more or less obviously towards an imaginary line prolonged through the centre of the wedge into the bark. Indications of this arrangement are seen at *g'* in fig. 32.

The usual aspect of the masses of cortical parenchyma separating the primary vascular wedges, as they appear in vertical tangential sections, is shown in several of the figures, but especially in figs. 27, 30, & 35, *h*. In these sections it appears as ordinary parenchyma, whilst in radial sections of the same tissue its cells exhibit a tendency to arrange themselves in semimural fashion, as seen at fig. 27, *h'*.

External to the cortical structures just described is another and yet more extensive one, which appears to have been the primitive tissue of these stems. I infer this from the fact that in the young twigs (figs. 24 & 25) it is the only cortical tissue observable, except the epidermal layer (*k*), and occupies the entire area between that layer and the central vascular bundle (*c*). Its thickness relative to the size of the stem is also well seen in fig. 23. It consists of a coarse but thin-walled parenchyma, the cells of which are of unequal sizes, but generally about ·005. The mean thickness of this layer in fig. 23 is about ·025. It appears distinctly in figs. 32, 33, & 34, *i*, investing both the vascular axis of the primary stem and the branch which is being given off from the latter; whilst in fig. 34, in which the vascular area of the branch is entirely separated from that of the main axis, it constitutes the chief portion of the separating layer. In the three sections just referred to, whilst we see the tissue in question enclosing the more internal layers of the bark and their associated vascular areas, it will also be noticed that in passing over the cellular radii which separate the six large vascular wedges it dips inwards towards the centre of the stem. This arrangement is well seen in fig. 34, *i'*, *i''*.

Another of the characteristic features of this very remarkable plant is found in the distinct epidermal layer (*k*) with which it is shown to be invested in figs. 23, 24, & 25. A more highly magnified representation of the same tissue, as seen in the transverse sections, but enlarged 284 diameters, is seen in fig. 28. Viewed in this aspect it consists of two somewhat irregular rows of cells, which are very distinctly different from those of the bark (*i*) which they immediately invest. Those of the outer bark (*i*) have their walls of a dark colour and mottled aspect—a condition apparently due to the carbonization of the cell-contents which characterized them when living. Those of the epidermis, on the other hand, are more clear and transparent, as if they had been originally devoid of all coloured protoplasm or other cell-contents. They are also smaller in size, averaging, in transverse sections, about ·008, and retain their regular form much more perfectly than the larger and softer cells underlying them. The distinction between these two tissues becomes yet more conspicuous when we turn to the longitudinal section, fig. 36. We here see that the epidermal layer (fig. 36, *k*) is separated from the cortical parenchyma by a sharply defined line, whilst its component cells are

elongated. They vary considerably in their vertical length, those delineated in fig. 36, *k* being longer and narrower than they are in some other portions of the section of which the figure represents a small part; but the tissue is always easily distinguished from that which it invests.

Exogenous growth.—The difference between the sections figs. 24 & 25, in which we have merely the primary vascular bundle, and fig. 23 and other similar figures, in each of which what is obviously a corresponding bundle (*c*) is surrounded by six diverging wedges composed of radiating laminæ of vessels separated by medullary rays, affords sufficient proof of the existence of exogenous growth in these plants. These wedges exhibit the same evidences of being the result of successive peripheral additions that we have already found in the instances of many other Carboniferous plants. This is especially the case with some, of part of one of which fig. 31 is a representation, enlarged 130 diameters. It is a portion of a transverse section of the same specimen as is represented in the figures 32, 33, & 34. We find at *e*, *e* the outer extremities of several vascular laminæ, separated by the medullary rays (*f*, *f*), whilst at *g* we have a portion of one of those crescentic masses of peculiar cellular tissue which I have already described as being located at the peripheral extremity (fig. 34, *g*) of each of the six primary vascular wedges. There is no mistaking the evidence that along the line (fig. 31, *e'*, *e'*) a conversion has been going on of the cells of this tissue into true vessels, destined to form outward extensions of the vascular laminæ (*e*, *e*). Oblique longitudinal sections show that the narrow cells (*e''*), which are here being elongated in a direction parallel to the transverse diameters of the vessels with which they are in contact, are also elongated in the vertical direction, and are assuming a vascular aspect. Hence it becomes clear that the cellular tissue *g* is, as I have already stated, a special meristem tissue possessing pseudo-cambial properties, and the active instrument in producing the peripheral vascular growths. It thus appears that in these plants the pseudo-cambial layer never becomes a continuous ring as in most of the other exogenously developed plants which I have already described, but that it remains permanently in the state in which it exists in the first year's growth of a Dicotyledonous Exogen, *i. e.* as a ring of detached masses, in which the interfascicular cambium has never been developed; affording another instance, in the palæozoic vegetable world, in which conditions that are temporary and transitional in ordinary exogens are rendered permanent ones.

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It is impossible to study this plant without being reminded of the Bignoniaceous Llianos of the Brazilian forests; but though in these latter plants the woody axis is primarily divided into four distinct radiating wedges, and though these four wedges continue to grow prominently in advance of the spaces occupied by the cortical tissues that separate them, yet even these latter spaces contain a true cambial layer, through the agency of which they become filled up with vascular tissues that gradually encroach peripherally upon the cortical structure; and as they advance, they destroy the perfect form of the Maltese cross which transverse sections of these woody axes exhibit. Hence the resemblance between my fossil and true Bignoniaceous Exogens is more apparent

than real, since in the former the radial inward prolongations of the bark (*h*) never become occupied by vascular structures, whilst, I need scarcely add, the morphology of the cortical layers in the two cases is altogether different.

Branches.—In the present state of our knowledge I am unable to ascertain whether figs. 24 & 25 are branches of stems like fig. 23, or correspond to its terminal portions; but be that as it may, I have obtained independent proof that at least one class of branches is given off from similar stems, besides which we have many indications of the existence of another and apparently very different set of secondary lateral vascular bundles. Figures 32, 33, & 34 represent three very instructive transverse sections of one stem, in which the various stages in the development of the branch can be easily traced. These sections were made at intervals of little more than the sixteenth of an inch apart. Fig. 32 is the lowest of the series. The vessels of the central axes have been partly destroyed, and the epidermal layer and some of the subjacent outer cortical layer are also wanting. In other respects the section exhibits in a beautiful manner the more characteristic features of this plant. The two primary vascular wedges (*c*, *c'*) also present much of their usual appearances; but we find that the inward prolongation of the cellular bark (*h'*) separating these two wedges, instead of attaining to its usual dimensions, is narrowed to two or three radial rows of cells (*h*), being encroached upon by a mass of obliquely inclined vessels (*x*), which exhibit every appearance of being given off from the left-hand side of the primary vascular wedge (*c*), and of ascending obliquely from right to left. In the next higher section (fig. 33) the two vascular wedges (*c'*, *c''*) have been pushed widely asunder, and the triangular area between them is now occupied by a number of meandering vessels intermingled with a little cellular tissue. These vessels are proceeding outwards to a semicircular mass of vessels, of which those occupying the centre, whence the others radiate, are arranged without order, like those of the central axis (*c*) of figs. 23 & 26; and the rest are distributed in radiating series, forming numerous exogenous laminæ and wedges separated by many medullary rays (*f*). On turning to the third section in the ascending series (fig. 34), we find that the two wedges (*c'*, *c''*) have resumed their normal positions, and that the wedge of cellular bark intervening between them exhibits little or no difference from the corresponding tissue separating the other vascular wedges of the section, save that one or two detached radiating laminæ of small vessels pass outwards through its parenchyma. The lateral vascular laminæ of the two woody wedges, which are in immediate contact with the intervening bark, have not quite recovered the regularity of radiating arrangement which characterizes them elsewhere. This disturbance of the order is especially seen near the peripheral margin of each wedge. The branch itself now consists of a normal central axis, with its exogenous wedges arranged around that centre, so as to form a complete circular cylinder, which is now entirely separated from the vascular portion of its parent stem by the intervention of a mass of the coarse outer cortical parenchyma (*i*). The radiating series of vessels constituting the exogenous portion of the branch are still seen to be separated by numerous medullary rays of nearly equal size, the separation of these vessels into the six groups seen in

the parent stem not having been perfectly accomplished. Nevertheless there are indications that such a separation is in progress. Thus we see at *h* a mass of cellular tissue separating the vascular masses on either hand of it; not only so, but we discover at the peripheries of three such vascular masses a tendency towards that convergence of the outer extremities of the newly forming vessels of each primary wedge which has been already described and illustrated by fig. 32, *g*. The largest of the vessels in this branch does not exceed ·0025 in diameter.

On glancing at fig. 33 the observer is strongly disposed to conclude that the meandering vessels radiating outwards from the parent stem to the half-formed branch were equally derived from the two wedges, *c'*, *c''*; but I believe that, primarily at least, this is not the case. I have already pointed out that in the lowest of the three sections (fig. 32) the aberrant vessels (*x*) unmistakably proceed from the wedge *c*, being separated from *c'* by the radiating extension of the inner bark (*h'*). I have another transverse section of the specimen from which the above three were made, which exhibits a second and similar branch, but which has been so bent in the plane of the section that, though the main stem is intersected transversely, the section cuts through the branch longitudinally. In this case the branch certainly proceeds solely from *one* of the neighbouring primary wedges. In all these sections the vessels of the secondary branches are much smaller than those of the parent stem. It is not impossible that as the branch develops, both the contiguous primary wedges may contribute some vascular elements towards its formation, as appears to be indicated by fig. 33.

In fig. 33 the peculiar cellular tissue which I have termed pseudo-cambial forms an almost continuous semicircular belt around that peripheral upper portion of the branch in which the vascular laminæ have assumed their normal radiating order. But in fig. 34, on the other hand, it has begun to concentrate itself into masses at the extremities of the incipient primary vascular wedges, as in the matured stem. This is especially the case at the four points *g*, *g*, *g*, *g*. It is obvious that these several points represent a corresponding number of incipient primary vascular wedges.

Having ascertained these facts, I turned with some interest to the well-known stems of the Bignoniaceæ, to see how far the orientation of their lateral branches corresponded with what I have just described. In these plants there is a distinct medulla, and the lateral twigs are given off in pairs. When this is about to take place, two of the four woody wedges constituting the Maltese cross exhibited by a transverse section of the stem become much broader than the other two, and a prolongation of the pith passes outwards through the centre of each of these enlarged wedges, and carries along with it an investing cylinder chiefly composed of sclerenchyma. Thus each branch springs *from the centre* of a woody wedge, and not from its sides, as in my fossil plant. It follows that in the *Bignoniæ* the areas occupied by the centripetal prolongations of the cortex separating the four arms of the cross take no part in the formation of the branch; whereas we have seen that in my fossil this area is largely concerned in its formation. In one point, however, there is a resemblance between the two cases. In the very

young lateral twig of *Bignonia* the ligneous axis is nearly cylindrical, when it must be invested by a complete ring of cambium; but this ring clearly becomes broken up, as growth advances, into four detached segments, corresponding to the peripheral extremities of the four large crucially disposed woody wedges seen in more matured stems. Hence in this case the cambial ring, primarily continuous, became an interrupted one. It subsequently again approximated to a continuous one by the development of interfascicular cambium. But whilst on these points there seems to be some analogy between the development of a Bignoniaceous twig and that of my fossil plant, there yet remains an additional distinctive feature. In the former a detached patch of cambium occupies the innermost extremity of each of the four centripetal prolongations of the inner bark which separate the woody wedges, so that these cortical radii are steadily encroached upon by four corresponding radii of wood, which are slowly growing outwards, following, but at a very great distance, the extensions of the four arms of the cross. Nothing like this occurs in my Carboniferous plant. In the latter the six centripetal extensions of the inner bark never become thus converted into a portion of the vascular cylinder.

Figures 37 & 38 represent two transverse sections of the vascular axes of stems of small size. The larger of these has a diameter of ·032, and the smaller one of ·017. The larger of these two sections is therefore only about two thirds the size of the corresponding vascular axes of the young branch in fig. 34, the diameter of which is about ·047, whilst the smaller one is but little more than one third of the diameter of the same branch. The vessels in figs. 37 & 38, like those of the branch referred to, have a maximum diameter of ·0025. I conclude that these two figures represent the vascular centres of two small branches deprived of their cortical layer. Their chief interest lies in the circumstance that fig. 37 exhibits but five primary vascular wedges, and fig. 38 but four; whereas every example which I have yet seen, where the stem has attained to what appears to be its normal dimensions, these primary wedges are six in number, as already described. The section of a nodule which contains the two stems (figs. 37 & 38) also contains a third one in their immediate vicinity, and which in all probability belonged to the same plant as the other two: its vascular axis has a diameter of rather more than ·1. It also has but five wedges; but one of them is so much broader than the rest as to make it exceedingly probable that it would eventually subdivide into two, and thus complete what appears to be the complementary number of six, characteristic of all matured stems.

The above description makes it obvious that in a very young stage of the development of the exogenous, vascular portion of a stem or branch, the differentiation of the vascular laminæ into the six distinct groups, which I have termed primary wedges, is very imperfect, the large radial masses of cellular tissue (*h*) which ultimately separate them being then little more than ordinary medullary rays. If this is true, the mural parenchyma composing them must retain its genetic properties as a meristem tissue, since they certainly become much broader, containing an increased number of cells, as they grow older.

Besides the remarkable branches which I have just described, I find clear evidence of the existence of another, and apparently very different, set of divergent vascular bundles, and which pass outwards through the large cellular radii (*h*) which separate the primary woody wedges. But I find it much more difficult to obtain a clear conception of the nature, origin, and distribution of these bundles than of those previously noticed. In fig. 30 there is represented a condition of which I have seen several examples. In the parenchyma (*h*) separating the two primary vascular wedges *d* and *d'* there is an obvious derangement of the usual condition of the cells of that parenchyma at *y*. The latter display an obvious disposition to be elongated radially, bending outwards to accompany a small bundle of vessels seen at *y*, which is here cut across by the tangential section somewhat obliquely. In fig. 35 we have a similar but more perfectly tangential section of one of the same cellular radii (*h*), with portions of two primary vascular wedges at *d*, *d'*. At *y* we again find a cluster of small vessels passing outwards. At *e*, *e'* we have some meandering vessels detached from direct connexion with each of the two primary bundles (*d*, *d'*), but which obviously contribute to swell the diameter of the intersected bundle, *y*. At *e''* we find a few vessels, separated from those of the primary bundle (*d'*) by a few mural cells of a medullary ray, and which appear to be descending to reach the bundle *y*, towards which their lower extremities bend away from the primary wedge, *d'*. In fig. 36 we again find a similar bundle (*y*) passing through the coarse parenchyma of the outer bark, apparently on its way to escape through the epiderm, *k*. Though I have seen in my sections several other similar indications of these bundles, none of my specimens throw any clear light upon them. That they are distinct from the branches previously described appears very possible; but what is their ultimate purpose I have not yet succeeded in ascertaining. If the vessels *e* and *e''* in fig. 35 really go to the bundle *y*, as they appear to do, there can be no doubt but that they are respectively derived from the two primary vascular wedges, *d* and *d'*. But I cannot yet determine satisfactorily whether the bundle *y* consists wholly of vessels, or of vessels mixed with cells derived from the inner cortical layer through which they emerge. There are indications that some of the cells of the latter are elongated radially to form a sort of sheath to the vessels. All these points are at present but obscurely indicated by my specimens; but the general features of these bundles differ so widely from those of the true branches represented by figs. 32, 33, & 34 as to leave little doubt that they have had a distinct nature, having probably been destined to supply either rootlets or leaves with vessels. Unfortunately my specimens of this very rare plant have hitherto been too few in number to enable me to obtain such a good radial section as might throw light upon these diverticula of the central vascular axis. At the same time it *may* be possible that these bundles pass outwards to become the central bundles of branches corresponding to figs. 24 & 25.

The question of the nature and probable affinities of this plant remains to be examined; and here, again, we have unfortunately to deal with much that is obscure. In the vascular character of its primary central axis (figs. 23–24, *c*) we are reminded of

the vascular axis of the fruit *Calamostachys Binneana* (Phil. Trans. 1874, p. 59 *et seq.*, figs. 33–39), of the stem of *Asterophyllites*, and of the medullary axis of the Lepidodendroid plants described and figured in my second memoir on the Plants of the Coal-measures (*loc. cit.* 1872, Plate 24. figs. 1 & 2). I have already given my reasons for regarding all these three groups of plants as Lycopodiaceous; and it is my conviction that the plant now described belongs to the same natural family. At the same time I need scarcely remark that it differs from all known recent Lycopodiaceæ. Several of the living Lycopods exhibit a defined epidermal layer, investing a cortical parenchyma composed of large cells full of chlorophyl. *Lycopodium alpinum* exhibits this condition; and in *Selaginella Martensii* a similar epiderm, composed of colourless cells, becomes very conspicuous at the margins of the leaflets, where it projects in comparatively large tooth-like, almost unicellular, hairs or spines. But none of these plants exhibit any thing that exactly resembles even the primary central vascular bundle of the fossil form. The nearest approach to it is perhaps to be seen in *Psilotum triquetrum*; but we have nothing resembling the exogenous growth of the six primary vascular wedges in any recent Lycopodiaceous stem. In the peculiar structure of its entire vascular axis this plant stands alone amongst the varied types found in the Carboniferous beds. In the structure of its central vascular axis, especially as seen in the young twigs (figs. 24 & 25), it bears a considerable resemblance to the *Lycopodium Renaultii* described by Professor Renault*; but in the other details of their respective structures I can find few, if any, resemblances between my plant and that of my distinguished friend. In the *L. Renaultii* its discoverer has as yet found no trace of the exogenous growth which is so characteristic of my example.

That the plant is a Cryptogam I think there can be no doubt. It presents no features that indicate a Dicotyledon. All its vessels are mere modifications of the spiral and barred tissue which constitute so universal a feature in the stems of the other Carboniferous Cryptogams. The sclerenchymatous prosenchyma of the woody rings of the Dicotyledons is entirely wanting to its woody zone. It possesses this feature in common with the *Calamites*, *Lepidodendræ*, *Asterophyllites*, and other Carboniferous Cryptogams which I have already described.

In one respect the plant under consideration is one of the most remarkable of any that I have yet seen. Though the largest stem that I have found does not exceed one eighth of an inch in diameter, which is the thickness of that represented in fig. 23, yet its exogenous development is complete. In criticising my views in an early stage of my inquiries, my friend Professor Thisleton Dyer expressed his conviction that these supposed exogenous growths were mere questions of size, and had no physiological meaning. But such cannot possibly be the case here. The axis of nearly every known living Lycopod has a diameter equal to that of the fossil before us; yet we find the exogenous structure of the latter as conspicuously developed as in the largest of the Lepidodendroid stems. Whatever

* "Étude de quelques végétaux silicifiés des environs d'Autun," Annales des Sciences Naturelles, 5e série, Bot., t. xii. (Cahier no. 3), pp. 82–85.

may be the meaning of the prevalence of exogenous development amongst the Cryptogams of the Carboniferous epoch, it clearly has no relation to mere size.

Since the plant now described is remarkably different from any hitherto noticed, I propose to assign to it the generic title of *Kaloxylon*, and to identify it with the name of our distinguished President as *Kaloxylon Hookeri*.

All the specimens which I have figured are from the Oldham Upper foot-coal. But I have found two or three sections of very young branches, in the condition of that represented in the upper part of fig. 34, amongst my sections of specimens from Burnt-island. This circumstance indicates that the genus has had a considerable vertical range, and hence may be expected to occur in some of the continental deposits like those of Autun and St. Etienne, whence I trust that M. Renault or M. de Grand-Eury will soon succeed in disinterring it.

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Myelopteris (*Medullosa* of Cotta).

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Plate 3. fig. 9. Transverse section of part of a petiole in which no gum-canals exist in contact with the vascular bundles. Enlarged 65 diameters.
Plate 1. fig. 10. Longitudinal section of a vascular bundle of fig. 9, exhibiting the elongated cells constituting the imperfect bundle-sheath. Enlarged 65 diameters.
Plate 2. fig. 11. Transverse section of a vascular bundle from the periphery of fig. 1, with very few vessels in it. Enlarged 65 diameters.

Plate 1. fig. 12. A spiral vessel from the specimen fig. 8. Enlarged 400 diameters.

Plate 3. fig. 13. Transverse sections of portions of two vessels (*d*) of the vascular bundle of a petiole, exhibiting part of the bundle-sheath at *e* and a detached fibrous bundle at *f*. Enlarged 350 diameters.

„ fig. 14. Transverse section of a vascular bundle from fig. 1, with enlarged gum-canal (*c*) and cellular bundle-sheath (*e*). Magnified 65 diameters.

„ fig. 15. Longitudinal tangential section of the cortical layer of a young rachis, with alternating bands of prosenchyma (*b*) and parenchyma (*a*). Enlarged 65 diameters.

Plate 2. fig. 16. Part of the hypodermal layer of the transverse section (fig. 1), showing the wedge-shaped bands of prosenchyma (*b*) projecting into the parenchymatous tissue, *a*. Enlarged 80 diameters.

Plate 4. fig. 17. A similar section to fig. 16, from Capt. AITKEN's specimen, showing the detached islets of hypodermic prosenchyma (*b'*, *b''*) and gum-canals at *c*, *c*.

Psaronius Renaultii.

Plate 3. fig. 18. Transverse section of a cluster of rootlets. Natural size.

Plate 4. fig. 19. Transverse section of the superficial cortical parenchyma of a stem, with the adventitious rootlets passing outwards through it. Enlarged 12 diameters.

Plate 3. fig. 20. Cluster of free rootlets, exhibiting numerous radicular epidermal hairs. Enlarged 12 diameters.

„ fig. 21. Portions of three rootlets, with their radicular hairs. Enlarged 40 diameters.

Plate 4. fig. 22. Central vascular bundle of a compressed rootlet, imbedded in condensed cellular tissue.

„ fig. 22*. Transverse section of a specimen from Mr. CARRUTHERS's cabinet, exhibiting a vascular bundle (*d*) of the stem enclosed in parenchyma. Natural size.

„ fig. 22**. The lower part of fig. 22*. Enlarged 8 diameters.

Kaloxylon Hookeri.

Plate 5. fig. 23. Transverse section of a matured stem. Enlarged 29 diameters.

„ fig. 24. Transverse section of a very young stem or branch, with the central vascular axis, but with no exogenous growths. Enlarged 24 diameters.

„ fig. 25. Similar section to fig. 24. Enlarged 24 diameters.

„ fig. 26. Obliquely transverse section of a matured stem deprived of its outer bark. Enlarged 36 diameters.

„ fig. 27. Tangential section of a vascular exogenous wedge made near its peripheral extremity, and showing the vertical medullary rays at *f*, *f*. Enlarged 60 diameters.

Plate 6. fig. 28. Transverse section of the outermost cortical layers, showing the double row of epidermal cells. Enlarged 200 diameters.

Plate 4. fig. 29. Radial longitudinal section of a matured stem passing through two vascular laminæ at *e* and *e'*, with the mural cells of the medullary ray separating the laminæ at *f*, *f*. Enlarged 130 diameters.

Plate 6. fig. 30. Tangential section of a matured stem intersecting the central vascular exogenous wedge (*d*) near the medullary vascular axis, the two more external ones (*d'*, *d''*) being intersected a little obliquely and nearer to their peripheral extremities, as in fig. 27. The centripetal cortical parenchyma separating the three vascular wedges is seen at *h*, *h*. Enlarged 65 diameters.

„ fig. 31. Transverse section of the peripheral portion of the vascular wedge of a matured stem, exhibiting several vascular laminæ (*e*, *e*) separated by medullary rays (*f*, *f*), and showing new vessels (*e'*, *e''*) forming in the pseudo-cambial layer (*g*, *g*). Enlarged 130 diameters.

„ fig. 32. Transverse section of a matured stem deprived of its outermost bark, but detaching laminæ of vessels at *x* from the vascular wedge to the right of the cortical lamina (*h'*) preparatory to the formation of a branch. Enlarged 30 diameters.

„ fig. 33. Transverse section of the same stem as fig. 32, but made a little higher up than that section. The branch has here attained a semicylindrical form, pushing aside the two vascular wedges (*c'*, *c''*), and has definite medullary rays (*f*, *f*) separating its radiating vascular laminæ. Enlarged 40 diameters. The pseudo-cambial masses are seen at *g*, *g*. Enlarged 30 diameters.

Plate 7. fig. 34. A third transverse section of the same stem made a little higher up than fig. 33. The branch has now attained its cylindrical form and become entirely free from the wedges (*c'*, *c''*), which have returned to nearly their normal positions. The vascular laminæ of the branch exhibit a tendency to arrange themselves into groups corresponding to the primary wedges of the parent stem. Enlarged 30 diameters.

„ fig. 35. Tangential section of two primary vascular wedges (*d*, *d'*), with a vascular bundle (*y*) passing outwards through the intervening cortical parenchyma (*h*). Enlarged 48 diameters.

„ fig. 36. Obliquely tangential section of the cortical portion of the stem (fig. 1), showing a vascular bundle (*y*) like that of fig. 35, passing outwards through the outer cortical layer (*i*). Elongated examples of the epidermal cells seen at *k*. Enlarged 48 diameters.

„ fig. 37. Section of a very small vascular axis, with but five primary wedges. Enlarged 80 diameters.

„ fig. 38. Similar section to the last, but with four primary wedges. Enlarged 80 diameters.

II. *The Optical Deportment of the Atmosphere in relation to the Phenomena of Putrefaction and Infection.* By JOHN TYNDALL, *F.R.S.*

Delivered orally January 13,—Received complete April 6, 1876.

§ 1. *Introduction.*

AN inquiry into the decomposition of vapours by light, begun in 1868 and continued in 1869*, in which it was necessary to employ optically pure air, led me to experiment on the floating matter of the atmosphere. A brief section of a paper published in the Philosophical Transactions for 1870† is devoted to this subject.

I at that time found that London air, which is always thick with motes, and also with matter too fine to be described as motes, after it had been filtered by passing it through densely packed cotton-wool, or calcined by passing it through a red-hot platinum-tube containing a bundle of red-hot platinum wires, or by carefully leading it over the top of a spirit-lamp flame, showed, when examined by a concentrated luminous beam, no trace of mechanically suspended matter. The particular portion of space occupied by such a beam was not to be distinguished from adjacent space.

The purely gaseous portion of our atmosphere was thus shown to be incompetent to scatter light.

I subsequently found that, to render the air thus optically pure, it was only necessary to leave it to itself for a sufficient time in a closed chamber, or in a suitably closed vessel. The floating matter gradually attached itself to the top and sides, or sank to the bottom, leaving behind it air possessing no scattering power. Sent through such air, the most concentrated beam failed to render its track visible.

I mention 'top' and 'sides,' as well as 'bottom,' because gravity is not the only agent, probably not the principal agent, concerned in the removal of the floating matter. It is practically impossible to surround a closed vessel by an absolutely uniform temperature; and where differences of temperature, however small, exist, air-currents will be established. By such gentle currents the floating particles are gradually brought into contact with all the surrounding surfaces. To these they adhere, and, no new supply being admitted, the suspended matter finally disappears from the air altogether.

The parallelism of these results with those obtained in the excellent researches of SCHWANN‡, SCHROEDER and DUSCH§, SCHROEDER himself‖, and PASTEUR¶ in regard to the question of "spontaneous generation," caused me to conclude that the power of scattering light and the power of producing life by the air would be found to go hand in hand.

* Proc. Roy. Soc. vol. xvii.

† Vol. clx. p. 337.

‡ Pogg. Ann. 1837, vol. xli. p. 184.

§ Ann. der Pharmacie, vol. lxxxix. p. 232.

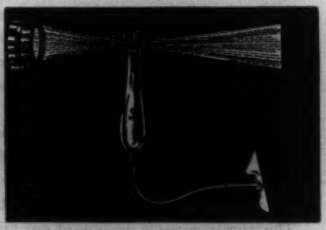
‖ Ann. der Pharmacie, vol. cix. p. 35.

¶ Ann. de Chim. et de Phys. 3rd series, vol. lxiv. p. 83.

This conclusion was strengthened by an experiment easily made and of high significance in relation to this question. It had been pointed out by Professor Lister, of Edinburgh *, that air which has passed through the lungs is known to have lost its power of causing putrefaction. Such air may mix freely with the blood without risk of mischief; and that truly great scientific Surgeon had the penetration to ascribe this immunity from danger to the filtering power of the lungs. Prior to my becoming acquainted with this hypothesis in 1869, I had demonstrated its accuracy in the following manner†.

Condensing in a dark room, and in dusty air, a powerful beam of light, and breathing through a glass tube (the tube actually employed was a lamp-glass, rendered warm in a flame to prevent precipitation) across the focus, a diminution of the scattered light was first observed. But towards the end of the expiration the white track of the beam was broken by a perfectly black gap, the blackness being due to the total absence from the expired air of any matter competent to scatter light. The experimental arrangement is represented in fig. 1, where *g* represents the heated lamp-glass, and *b* the gap cut out of the beam issuing from the lamp L. The deeper portions of the lungs were thus proved to be filled with optically pure air, which, as such, had no power to generate the organisms essential to the process of putrefaction‡.

Fig. 1.



It seemed that this simple method of examination could not fail to be of use to workers in this field. They had hitherto proceeded less by sight than by insight, being in general unable to see the physical character of the medium in which their experiments were conducted. But the method has not been much turned to account; and this year I thought it worth while to devote some time myself to the more complete demonstration of its utility.

I also wished to free my mind, and if possible the minds of others, from the uncertainty and confusion which now beset the doctrine of "spontaneous generation." Pasteur has pronounced it "a chimera," and expressed the undoubting conviction that this being so it is possible to remove parasitic diseases from the earth. To the medical profession, therefore, and through them to humanity at large, this question, if the

* Introductory Lecture before the University. † Proc. Roy. Inst. vol. vi. p. 9.

‡ "No putrefaction," says Cohn, "can occur in a nitrogenous substance if it be kept free from the entrance of new *Bacteria* after those which it may contain have been destroyed. Putrefaction begins as soon as *Bacteria*, even in the smallest numbers, are accidentally or purposely introduced. It progresses in direct proportion to the multiplication of the *Bacteria*; it is retarded when the *Bacteria* (for example, by a low temperature) develop a small amount of vitality, and is brought to an end by all influences which either stop the development of the *Bacteria*, or kill them. All bactericidal media are therefore antiseptic and disinfecting."—*Beiträge zur Biologie der Pflanzen*, zweites Heft, 1872, p. 203.

illustrious French philosopher be correct, is one of the last importance. But PASTEUR's labours, which have so long been considered models by most of us, have been subjected to rough handling of late. His reasoning has been criticised, and experiments counter to his have been adduced in such number and variety, and with such an appearance of circumstantial accuracy, as to render the evidence against him overwhelming to many minds. This, I have reason to know, has been the effect wrought, not only upon persons untrained in science, but also upon biologists of eminence both in this country and America. The state of medical opinion in England is correctly described in a recent Number of the 'British Medical Journal,' where, in answer to the question, "In what way is contagium generated and communicated?" we have the reply that, notwithstanding "an almost incalculable amount of patient labour, the actual results obtained, especially as regards the manner of generation of contagium, have been most disappointing. Observers are even yet at variance whether these minute particles, whose discovery we have just noticed, and other disease-germs, are always produced from like bodies previously existing, or whether they do not, under certain favourable conditions, spring into existence *de novo*."

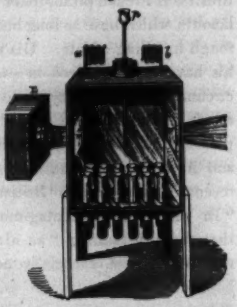
With a view to the possible diminution of the uncertainty thus described, I beg without further preface to submit to the Royal Society, and especially to those who study the etiology of disease, the following description of the mode of procedure followed in this inquiry, and of the results to which it has led.

§ 2. *Method of Experiment.*

A chamber, or case, was constructed, with a glass front, its top, bottom, back, and sides being of wood. At the back is a little door which opens and closes on hinges, while into the sides are inserted two panes of glass, facing each other. The top is perforated in the middle by a hole 2 inches in diameter, closed air-tight by a sheet of india-rubber. This sheet is pierced in the middle by a pin, and through the pin-hole is passed the shank of a long pipette ending above in a small funnel. A circular tin collar, 2 inches in diameter and 1½ inch deep, surrounds the pipette, the space between both being packed with cotton-wool moistened by glycerine. Thus the pipette, in moving up and down, is not only firmly clasped by the india-rubber, but it also passes through a stuffing-box of sticky cotton-wool. The width of the aperture closed by the india-rubber secures the free lateral play of the lower end of the pipette. Into two other smaller apertures in the top of the cupboard are inserted, air-tight, the open ends of two narrow tubes, intended to connect the interior space with the atmosphere. The tubes are bent several times up and down, so as to intercept and retain the particles carried by such feeble currents as changes of temperature might cause to set in between the outer and the inner air.

The bottom of the box is pierced with two rows of holes, six in a row, in which are fixed, air-tight, twelve test-tubes, intended to contain the liquid to be exposed to the action of the moteless air.

Fig. 2.



The arrangement is represented in fig. 2, where *w w* are the side windows through which the searching beam passes from the lamp L across the case C; *p* is the pipette, and *a b* are the bent tubes connecting the inner and outer air. The test-tubes passing through the bottom of the case are seen below.

On the 10th of September this case was closed. The passage of a concentrated beam across it through its two side windows then showed the air within it to be laden with floating matter. On the 13th it was again examined. Before the beam entered, and after it quitted the case, its track was vivid in the air, but within the case it vanished. Three days of quiet sufficed to cause all the floating matter to be deposited on the interior surfaces, where it was retained by a coating of glycerine, with which these surfaces had been purposely varnished.

§ 3. *Deportment of Urine.*

The pipette being dipped into the tubes, fresh urine was poured into eight of them in succession on the 13th of last September. Each tube was about half-filled with the liquid. The tubes were then immersed in a bath of brine, raised to ebullition, and permitted to boil for five minutes. Aqueous vapour rose from the liquid into the chamber, where it was for the most part condensed, the uncondensed portion escaping, at a low temperature, through the bent tubes at the top. Before the brine was removed little stoppers of cotton-wool were inserted in the bent tubes, lest the entrance of the air into the cooling-chamber should at first be forcible enough to carry motes along with it. As soon, however, as the ambient temperature was assumed by the air within the case the cotton-wool stoppers were removed.

The front and back of this chamber were squares of 14 inches the side, the depth of the chamber being 8·5 inches. It contained, therefore, 1666 cubic inches of air, which had unimpeded access to the liquid in the tubes. No stoppers were employed. The air was unaffected by calcination, or even by filtering. Neither cotton-wool nor hermetic sealing was resorted to. Self-subsidence was the only means employed to rid the "untortured" air of its floating matter.

A second series of eight tubes were filled at the same time with the same liquid, and subjected to the same boiling process. The only difference between the two series was, that these latter tubes were placed in a stand beside the former and exposed to the common air of the laboratory.

For the sake of distinction I will call the tubes opening into the case the *protected* tubes, and those opening into the common air the *exposed* tubes.

On the 17th of September all the protected tubes were bright and clear, while all the exposed tubes were distinctly turbid. Specks of mould, moreover, were in every

case seen on the surface of the exposed liquid. These waxed daily larger, and finally formed a thick layer on the top of every column. The liquid changed from a pale sherry to a reddish-brown colour, some of the tubes being more deeply tinged than others.

On the 27th of September I provided myself with a microscope having a magnifying-power of 1200 diameters. Under its scrutiny the turbidity of the liquid immediately resolved itself into swarms of *Bacteria* in active motion. Cohn correctly explains the turbidity. The index of refraction of the *Bacterium* being slightly different from that of the surrounding medium, a scattering of light is the consequence. This scattering, however, and the opalescence it produces, are practically independent of the motions of the *Bacteria*.

Since the date here referred to the exposed liquid has been frequently examined, both with the eye and with the microscope. To the former it is thickly turbid, to the latter it is swarming with life. Its smell is putrid. *All this time the protected tubes exhibit a liquid perfectly unchanged in appearance.* For four months it has remained as transparent and of as rich a colour as the brightest Amontillado sherry.

On the 1st of October another experiment similar in principle to that just described was begun. Fresh urine was employed, and a much smaller case. The capacity of the latter was 451 cubic inches; and three test-tubes, instead of twelve, were passed air-tight through its bottom. Like those in the larger chamber they were filled by a pipette, and boiled for five minutes in a bath of brine. Beside them were placed three other tubes containing the same liquid treated in exactly the same way, but exposed to the common air. On the 5th all the exposed tubes were turbid, and found by microscopic examination to be swarming with *Bacteria*. The colour of the exposed liquid changed from a pale sherry colour to a brown orange. On the 25th the tubes were again examined, and found full of *Bacteria*. Two months subsequent to this latter date the infusion, diminished by evaporation, was found well charged with Bacterial life.

While this process of putrefaction was going on outside, the tubes opening into the moteless air of the case remained perfectly clear.

The chamber represented in fig. 2, and above described, was the first operated on, and the liquid is shown by the draughtsman as filling only a small portion of the test-tubes. This smallness of volume is in part due to evaporation. Test-tubes 1·2 inch wide and 9 inches long were, in all subsequent experiments, nearly filled with the infusions. Strong in the first instance, these were sometimes kept until slow evaporation through the open tubes at the top of the case had reduced them to one third or one fourth of their original volume. Each experiment, therefore, was, in reality, a series of experiments, extending over months, on infusions of different strengths, the concluding ones of the series attaining a very high degree of concentration. In fig. 2 the portion of the tubes within the case ought to be less than one half of what it is there shown to be.

§ 4. *Mutton-Infusion.*

A case was constructed to contain six test-tubes. It, like the others, had a front of glass, side windows, and a back door. Its capacity was 857 cubic inches. It was sealed up on the 21st of September, and found free from floating matter on the 24th. Lean mutton, cut into small pieces, was digested for four hours in water of a temperature of 120° F. The infusion was then carefully filtered, and introduced into the six test-tubes by a pipette which was never removed from the case.

The mutton-juice was of a fine ruby colour; but on boiling, its albumen was precipitated, subsequently sank, and carried the colouring-matter with it. The supernatant liquid was perfectly clear. The frothing was considerable when the boiling began. Beside this case was placed a stand containing six test-tubes filled with the same infusion, but exposed to the common air.

On the 27th all the outside flasks were perceptibly turbid; on the 28th they were found well filled with *Bacteria*, which on the 30th had increased to astonishing swarms. On the 15th of October the tubes were again examined, and found charged with undiminished life. They remained thus "putrid" until the 14th of November.

During the whole of this time the infusion in contact with the moteless air of the chamber remained as clear as distilled water.

On the 14th of November I infected one of the clear tubes by introducing into it through the pipette a few drops of mutton-infusion which had been prepared and exposed upon the 12th of November, and which two days had sufficed to render turbid. On the 15th the inoculated infusion showed signs of turbidity, and on the 16th putrefaction had actively set in, the liquid being thickly muddy and full of life.

With a moteless chamber and three tubes, experiments were subsequently made on a second infusion of mutton. In this case, however, the infusion was boiled, its albumen was precipitated, and removed by filtration prior to its introduction into the chamber. The pellucid liquid was introduced on the 1st of October, boiled for five minutes in the brine-bath, and abandoned to the air of the case. A series of exposed tubes containing the same infusion, similarly treated, was placed beside the protected ones. On the 4th all the outside tubes were muddy and swarming with *Bacteria*. Schroeter and Cohn have shown that different colours are produced by different kinds of *Bacteria*. In the three exposed tubes here referred to a yellow-green pigment was developed.

Up to the present date, or for more than three months after its preparation, the infusion, considerably diminished by evaporation, remains in all the protected tubes as clear as at first.

§ 5. *Beef-Infusion.*

A beef-steak, after having its fat removed, was cut up into small pieces, and digested for three hours at a temperature of 120° F. The liquid was then poured off, boiled, and filtered. It was as clear and colourless as pure water. On the 4th of October it was

introduced into three tubes protected by a chamber of 451 cubic inches capacity. It was boiled for five minutes in a brine-bath. Three exposed tubes, containing the same infusion, were placed beside the protected ones. On the 5th the exposed tubes showed signs of haziness, on the 6th they were turbid, of a green colour, and filled with *Bacteria*. They have maintained their muddiness, colour, and swarming life up to the present time.

While the exposed beef-infusion putrified in this way, all the protected infusions remained perfectly sweet and clear.

§ 6. *Haddock-Infusion.*

The haddock was cut up and digested on the 24th of September; it was afterwards introduced into six tubes, protected by a chamber. On boiling, its albumen, like that of the mutton first referred to, coagulated and sank to the bottom, leaving a perfectly clear liquid behind. Six exposed tubes filled with the same infusion were placed beside the six protected ones.

On the 27th the exposed tubes were all turbid and swarming with *Bacteria*. On the 29th one of the tubes showed a fine green colour; three other tubes showed the same colour afterwards. The vivacity of the organisms was extraordinary, and their shapes various. They darted rapidly to and fro across the field, clashing, recoiling, and pirouetting—rendering it, indeed, difficult to believe in the vegetable nature which the best microscopists assign to them.

For nearly three weeks the protected tubes remained perfectly clear. To gain room, the case was subsequently shifted, and soon afterwards one of the six tubes became turbid. Something, doubtless, had been shaken into it from the top of the chamber.

For more than a month this single infected flask remained in company with the five healthy ones. The air containing the products of putrefaction had free access to the whole of them, but there was no spread of the infection. As long as the organisms themselves were kept out of the flasks, the "sewer-gas" developed by the putrefaction had no infective power. On the 14th of November I infected two perfectly pellucid tubes with haddock-infusion which, after boiling, had been exposed for two days to the air. On the 15th the two tubes had obviously yielded to the infection. On the 16th disease, if I may use the term, had completely taken possession of them. Into one of them only one or two drops of the turbid infusion had fallen, while ten times this amount was introduced into the other. Nevertheless on the 16th both appeared equally turbid. The infection acted exactly like the virus of smallpox, a small quantity of which will in the long run produce the same effect as a large one.

§ 7. *Turnip-Infusion.*

Turnip-juice had a special interest for me in consequence of the important part it plays in the experiments of Dr. Bastian. I turned to it with the anxious desire to learn whether the statements made concerning it were correct.

The conditions laid down as to the strength of the solution, the temperature to be

maintained during the time of digestion, and the time it was to be maintained* were scrupulously adhered to. Thus the turnip was cut into thin slices, and digested for four hours in a beaker of water immersed in a water-bath kept at a temperature close to 120° Fahr. The infusion was then carefully filtered, introduced through a pipette into its case, and boiled there for five minutes. Six protected test-tubes were charged with the infusion on the 24th of September, while six other tubes were placed on a stand outside, and exposed to the common air of the laboratory.

On the 27th the exposed tubes were distinctly turbid, and on microscopic examination were found peopled with *Bacteria*. The protected tubes, on the contrary, were perfectly clear. A little distilled water had been added to one of the outer tubes. The germinal matter, whatever it may be, must have been copious in the water; for the tube to which it was added far exceeded the other two in the rapidity of life-development. On the 30th this tube contained *Bacteria* in swarms, of small size, but of astonishing activity. The other tubes also were fairly charged with organisms, larger and more languid, but not at all so numerous as in the watered tube. On the 5th of October some of the exposed tubes began to clear; as if the *Bacteria* had died through lack of nutriment, and were falling as a thick sediment to the bottom.

During these changes the protected tubes were visibly unaltered, the liquid within every one of them remaining as clear as it had been on the day of its introduction.

In this instance I was specially anxious to verify the result by repetition. Two other cases were therefore fitted up to contain three tubes each, and instead of a door a movable panel was placed at the back. After two or three days' rest both cases were found free from floating matter, and on the 1st of October the turnip-infusion was introduced, and boiled for five minutes in a bath of brine.

In the former experiment the temperature of digestion was maintained by keeping the beaker containing the turnip in a bath of warm water. In the present instance the turnip was sliced in a dish and placed before a fire. An occult but efficient power like that already ascribed to the actinic rays†, might, I thought, be ascribed to radiant heat, and I therefore copied to the letter the mode of digesting pursued by Dr. Bastian.

Adjacent to the closed cases was placed a series of three exposed tubes, containing a liquid prepared in precisely the same way. On the 4th of October the exposed tubes were all turbid, and swarmed with *Bacteria*. In two of the tubes they were distinctly more numerous and lively than in the third. Such differences between sensibly conterminous tubes, containing the same infusion, are frequent. On the 9th, moreover, the two most actively charged tubes were in part crowned by beautiful tufts of mould. This expanded gradually until it covered the entire surface with a thick tough layer, which must have seriously intercepted the oxygen said to be necessary to Bacterial life. The *Bacteria* lost their translatory power, fell to the bottom, and left the liquid between them and the superficial layer clear.

* Beginnings of Life, vol. i. p. 357, note.

† Nature, vol. iii. p. 247.

Another difference, pointing to differences in the life of the air, was shown by these tubes. The turbidity of the two mould-crowned ones was colourless, exhibiting a grey hue. The third tube, the middle one of the three, contained a bright yellow-green pigment, and on its surface no trace of mould was to be seen. It never cleared, but maintained its turbidity and its Bacterial life for months after the other tubes had ceased to show either. It cannot be doubted that the mould-spores fell into this tube also, but in the fight for existence the colour-producing *Bacteria* had the upper hand. Six other tubes, similarly exposed, showed the grey muddiness: all of them became thickly covered with mould, under which the *Bacteria* died or passed into a quiescent state, fell to the bottom, and left the liquid clear.

Up to the 13*th of October the purity of the six protected tubes remained unimpaired.*

Here a complementary experiment was made. It remained to be proved that those long-dormant clear infusions had undergone no change which interfered with their ability to develop and maintain life. On the 13th, therefore, the small panel was removed from the back of one of the cases, and with three new pipettes specimens were taken from the three tubes within it. The closest search revealed no living thing. The air of the laboratory being permitted to diffuse freely into the case, on the day after the removal of the panel the test-beam showed the case to be charged with floating matter.

The access of this matter was the only condition necessary to the production of life; for on the 17*th all the tubes were muddy and swarming with* Bacteria.

A similar experiment, subsequently made, revealed to me some of the snares and pitfalls which await an incautious worker on this question. The chamber already referred to as containing six tubes, filled with turnip-juice, preserved the infusion clear for a month. On the 21st of October the back door of the chamber was opened, and specimens of the clear infusion were taken out for examination by the microscope. The first tube examined showed no signs of life. This result was expected, but I was by no means prepared for the deportment of the second tube. Here the exhibition of life was monstrously copious. There were numerous globular organisms, which revolved, rotated, and quivered in the most extraordinary manner. There were also numbers of lively *Bacteria* darting to and fro. An experimenter who ponders his work and reaches his conclusions slowly, cannot immediately relinquish them; and in the present instance some time was required to convince me that no mistake had been made. I could find none, and was prepared to accept the conclusion that in the boiled infusion, despite its clearness, life had appeared.

But why, in the protected turnip-infusion, which had been examined on the 13th of October, could no trace of life be found? In this case perfect transparency was accompanied by an utter absence of life. The selfsame action upon light that enabled the *Bacteria* to show themselves in the microscope must, one would think, infallibly produce turbidity. Why, moreover, should life be absent from the first member of the present group of tubes? I searched this again, and found in it scanty but certain signs

of life. This augmented my perplexity. A third tube also showed scanty traces of life. I reverted to the second tube, where life had been so copious, and found that in it the organisms had become as scanty as in the others. I confined myself for a time to the three tubes of the first row of the six, going over them again and again; sometimes finding a *Bacterium* here and there, but sometimes finding nothing. The first extraordinary exhibition of life it was found impossible to restore. Doubtful of my skill as a microscopist I took specimens from the three tubes and sent them to Prof. Huxley, with a request that he would be good enough to examine them.

On the 22nd the search was extended to the whole of the tubes. Early in the day lively *Bacteria* were found in one of them; later on, not one of the six yielded to my closest scrutiny any trace of life. On the evening of the 22nd a note was received from Prof. Huxley stating that a careful examination of the specimens sent to him revealed no living thing.

Pipettes had been employed to remove the infusion from the test-tubes. They were short pieces of narrow glass tubing, drawn out to a point, with a few inches of india-rubber tubing attached to them. This was found convenient for bending so as to reach the bottom of the test-tubes. Suspicion fell upon this india-rubber. It was washed, the washing-water was examined, but no life was found. Distilled water had been used to cleanse the pipettes, and on the morning of the 23rd I entered the laboratory intending to examine it. Before dipping the pipette into the water I inspected its point. The tiniest drop had remained in it by capillary attraction from the preceding day. This was blown on to a slide, covered, and placed under the microscope. An astonishing exhibition of life was my reward. Thus on the scent, I looked through my pipettes, and found two more with the smallest residual drops at the ends; both of them yielded a field rampant with life. The *Bacteria* darted in straight lines to and fro, bending right and left along the line of motion, wriggling, rotating longitudinally, and spinning round a vertical transverse axis. Monads also galloped and quivered through the field. From one of these tiny specks of liquid was obtained an exhibition of life not to be distinguished from that which had astonished me on the 21st.

Obviously the phenomenon then observed was due to the employment of an unclean pipette. Equally obvious is it that in inquiries of this nature the experimenter is beset with danger, the grossest errors being possible when there is the least lack of care.

The door of this case had been opened with a view to testing the capacity of the infusions within it to develop and maintain life. *For four weeks they had remained perfectly clear.* Two days after the door was opened and the common laboratory air admitted all six tubes were turbid, and swarming with *Bacteria*. Some of them were very long, and their wriggling and darting hither and thither very impressive.

The chamber here referred to was again thoroughly cleaned, sealed, and permitted to remain quiet until its floating matter had subsided. On the 17th of November a fresh infusion of turnip was introduced into it through the pipette, boiled in an oil-bath, and again abandoned to the air of the case.

Up to the present time the infusion in every tube of the six remains as clear as it was on the day of its introduction.

Six other tubes charged with the same infusion, boiled in the same way, became turbid in a few days, and subsequently covered with thick layers of *Penicillium*.

§ 8. *Hay-Infusion.*

This infusion has been credited with a power of spontaneous generation similar to that ascribed to turnip-juice. The hay being chopped into short lengths was digested for four hours in water kept at a temperature of 120° Fahr. On the 24th of September the filtered infusion was introduced into its chamber, and boiled there for five minutes. Six tubes were charged with the protected liquid, while six other tubes, filled with the same infusion, were placed on a stand outside the case.

On the 27th the inside flasks were clear, the outside ones faintly turbid. On the 28th spots of mould appeared upon all the exposed surfaces. The infusion in one of the tubes had been diluted with distilled water, and in it the development of life was far more rapid than in the five others; all of them, however, on the 28th contained *Bacteria*.

On the 29th I noticed a larger organism than the *Bacteria* moving rapidly to and fro across the field, the drop containing it being taken from the dilute infusion. Several of them were seen upon the 30th gambolling among the smaller *Bacteria*, appearing bright or dark as they sank or rose in the liquid, a film of which, large as they looked, was to them an ocean. Swarms of *Bacteria* were seen on the 2nd of October, their translatory motions being so rapid and varied, and guided by so apparent a purpose, as to render it difficult to believe that they could be any thing else than animals. On the 15th there was a marvellous exhibition of the larger Infusoria, which appeared to have driven the *Bacteria* from their habitat, as few of them were to be seen. My inability to find the larger creatures a second time in such numbers perplexed me, causing me to conclude that I had accidentally alighted upon a colony of them. Subsequent experience with the pipettes already described pointed, however, to another source.

While three days sufficed to break down the purity, and to fill with Bacterial life, the six exposed tubes, *the six protected ones remained for more than three months as clear and healthy as they were on the day the infusion was poured into them.* Neither a trace of mould upon the surface of any one of them, nor a trace of turbidity in its mass, was to be seen.

Into another case containing three test-tubes a very strong infusion of hay was introduced on the 1st of October. It was boiled for five minutes, and then abandoned to the air of the case. Three other tubes exposed to the laboratory air were placed on a stand beside the case. The colour of the infusion was very deep, but it was quite transparent. One of the outer tubes was diluted with distilled water. On the 3rd the infusion in this tube was turbid, the others remaining clear. The germinal matter had in some way or other

invaded the distilled water, and made its action rapid. The dilute infusion contained multitudes of *Bacteria*, many motionless, but many moving rapidly about. On the 4th of October all the tubes swarmed with *Bacteria*. They continued muddy till the middle of November, when they were employed for experiments on infection.

Throughout the whole of this time the protected tubes remained unchanged.

With regard to infection, it may be stated here that the merest speck of a vegetable infusion containing *Bacteria* infects all animal infusions, and *vice versâ*. The bursting of a bubble infects an infusion reached by the spray. It is the envelope, and not the gas of the bubble, which produces this result.

Other experiments on hay-infusions, acid, neutral, and alkaline, placed in contact with air purified in various ways, yielded the same negative result.

§ 9. *Infusion of Sole.*

The fish was cut up and digested for three hours in water kept at 120° Fahr. On the 17th of November it was introduced into a case containing three test-tubes, and boiled there for five minutes. Three other tubes hung outside the case were exposed to the ordinary laboratory air.

The three exposed tubes were feebly but distinctly cloudy on the 19th. On the 22nd they were all thickly turbid. Scattered spots of *Penicillium* then appeared on two of them, while the third tube, which stood between these two, kept the *Penicillium* down. This central tube contained the pigment-forming *Bacteria*, which have frequently shown a singular power in preventing the development of mould. For nearly two months the central tube has successfully withstood this development, while its two neighbours are covered by a matted layer of *Penicillium*.

During the whole of this time the protected infusion continued as clear and colourless as distilled water.

§ 10. *Liver-Infusion.*

On the 10th of November the infusion was prepared by the process of digesting already so often described. It was introduced into a case containing three protected tubes, and boiled there for five minutes in the brine-bath. Hung on to the chamber at the same time were three tubes containing the same infusion, but exposed to the common air. On the 13th *Bacteria* were numerous in the exposed tubes, and soon afterwards all three of them became thickly muddy and putrescent. They continued so for months.

The protected tubes, on the contrary, showed throughout a bright yellow liquid, as transparent as it was on the day of its introduction into the case.

§ 11. *Infusions of Hare, Rabbit, Pheasant, and Grouse.*

For the sake of economy, as so many of them were employed, the shape of the cases was subsequently varied. The rounded end of a tall glass shade was cut off, so as to convert the shade into a hollow cylinder (S, fig. 3), open at both ends. This was set

upright on a wooden stand, and cemented to it air-tight. Through the stand passed three large test-tubes (shown in the figure) also air-tight. To the top of the cylinder was cemented a circular piece of wood, the middle of which was occupied by a pipette, *p*, passing first through india-rubber and then through a stuffing-box, *o*, of cotton-wool moistened by glycerine*. The air within the case was connected with the air without by means of the open bent tubes *a* and *b*.

Fig. 3.

In the first experiments made with these cases defects of construction were revealed during the boiling of the infusions. But increased experience enabled my assistant to render them secure. The floating matter within the cases having been permitted to subside, into four of them, on the 30th of November, infusions of hare, rabbit, pheasant, and grouse were introduced. They were boiled in the usual way, and abandoned to the air of the case. Outside each case, and hung on to it, were three test-tubes of the same size and containing the same infusion as that within.

Examined on Christmas-day, the following were the observed results:—

Pheasant.—The three interior tubes perfectly limpid; the three exposed ones turbid and covered with *Penicillium*.

Grouse.—The same as pheasant.

Hare.—The same as grouse and pheasant.

Rabbit.—The three interior tubes covered with tufts of particularly beautiful *Penicillium*, some of the tufts striking deep into the liquid. In two out of the three tubes, moreover, mycelium was flourishing below. All the outer tubes were, as usual, turbid and covered with *Penicillium*.

Is this, then, a case of spontaneous generation? Without further evidence no cautious worker would draw such a conclusion. Opposed to this isolated instance stand all the others mentioned in these pages, and their proper action on the mind is to compel the closest scrutiny before accepting this apparent exception as a real one. Subjected to such scrutiny, it appeared that of the four shades the one containing the rabbit-infusion, and that only, had yielded to the heat of boiling. The shade had been fastened upon its slab with plaster and cement, which became so loose during the boiling that the steam issued from the chinks. But crannies which could permit steam to escape could permit air to enter, and to the presence of such air the appearance of the *Penicillium* was doubtless due.

I did not, however, rest content with mere inference, but tested the rabbit-infusion by placing three fresh tubes of it in one of the firmer cases first described. It was introduced and boiled on the 5th of January, three other tubes filled with the same boiled

* In the earlier experiments the india-rubber formed the bottom of the stuffing-box, where particles were sometimes detached from it by the motion of the pipette. To prevent this the positions of wool and rubber were afterwards reversed.

infusion being exposed on the same day to the ordinary air. The three protected tubes remained clear for three months, while in three days the three exposed ones were charged with *Bacteria*.

Salmon.—The colouring-matter of this fish did not at all affect the infusion; indeed no better example of original freedom from colour or opalescence, and of persistent purity in contact with the moteless air, has occurred to me than salmon-infusion. It was introduced into a cylindrical case on the 13th of December, where it continued for months to show the brilliant transparency exhibited at first. Three unprotected tubes, on the other hand, became turbid and covered with mould in a few days.

Hops.—One tube of this infusion was protected simply by a lamp-glass, corked and cemented above and below. Through the lower cork passed the single test-tube, air-tight; while through the upper one passed the pipette and the bent tubes intended to connect the outer and the inner air. The infusion was prepared and introduced on the 28th of October. In a few days the exposed tube was found turbid and covered with mould; the protected tube, on the contrary, remained clear for several months.

Tea and Coffee.—One tube of each was protected by a lamp-glass similar to that employed in the infusion of hops. Both were prepared on the 28th of October, exposed tubes being hung up at the same time. The protected tea has remained clear, while the exposed tea is turbid and covered with mould. Both the exposed coffee and the protected coffee are turbid and covered with mould.

The remarks already made with regard to the rabbit-infusion apply here. The case is one, not for the hasty admission of spontaneous generation, but for further scrutiny. I examined the apparatus as it stood. The pipette used to introduce the coffee (and this one only of the three employed in these experiments) rested against the outer edge of the tube containing the infusion. This had in part evaporated, had been in part condensed, and had trickled down the pipette so as to form a small drop at the point where pipette and tube touched each other. The drop had virtually washed the outer surface of the pipette, carrying with it, in part, such matter as might have attached itself to that surface. A portion of this washing-water reaching the infusion was doubtless the origin of the life observed. The sure test, however, was the repetition of the experiment under conditions which should exclude this source of error. On the 27th of December accordingly two tubes protected by lamp-glasses were prepared, two other tubes of the infusion being exposed to the air. The former remained clear for months, the latter in the same number of days became turbid and covered with *Penicillium*.

§ 12. *Infusions of Codfish, Turbot, Herring, and Mullet.*

With a view of causing these experiments on moteless and mote-laden air to run parallel with others made with hermetically-sealed tubes, to be described further on, I added the fish named in the heading of this section to the other substances examined. The mullet was introduced into its case on the 3rd of January. The warm air had, however, so acted on the wood of the case, which had been employed in former experiments,

that the water of condensation trickled from a chink in the bottom. The other cases were mended as far as possible, and into them the infusions were introduced on the 4th of January. Each case, as before, was provided with three exposed tubes for comparison with the three protected tubes within. On the morning of the 6th the exposed turbot-infusion was clear in all the tubes; a few hours subsequently two out of the three became cloudy; while on the 7th *Bacteria* had taken possession of all of them. All the unprotected tubes of codfish were cloudy on the 6th, more cloudy on the 7th, and covered with a soapy layer upon the 8th. The three exposed herring-tubes were also cloudy on the 6th, the cloudiness advancing afterwards to thicker turbidity. The mullet gave way in the same manner. For more than three months the protected tubes, including even the imperfect chamber which protected the mullet-infusion, have remained as clear as they were upon the day of their introduction.

To these fish-infusions may be added others of eel and oyster. Two tubes of each, protected by lamp-glasses, were charged on the 27th of December. They remain unchanged. Two other pairs of tubes, prepared in the same way and exposed to the laboratory air, are turbid and covered with *Penicillium*.

13. *Infusions of Fowl and Kidney.*

Three tubes of the fowl-infusion were introduced into a case, and boiled there for five minutes, on the 4th of January. Three similar tubes were at the same time exposed to the air. On the 6th all the outer tubes were cloudy, the cloudiness becoming denser on the following days, while disks of *Penicillium* began to form on the exposed surfaces. It was found exceedingly difficult to obtain a clear infusion of kidney. The liquid, after it had passed through a dozen filters, was still quite muddy. With considerable labour and care, and by the employment of 200 filters, the mechanically suspended matter was at length removed, and a hyaline infusion obtained. It was introduced into its case, to which three exposed tubes were attached, on the 4th of January. On the 7th the latter were perceptibly cloudy, on the 8th distinctly so, while specks of mould rested upon them all. The protected tubes, on the contrary, have for months maintained their transparency undimmed*.

The entire number of experiments made to illustrate the association of scattered light and Bacterial and fungoid life are not here recounted. Whiting, for example, may be added to the fish, and pork to the flesh examined, while many of the other substances have been tested oftener than I have thought it necessary to record. The method of boiling was also varied in a manner which may claim a passing reference here.

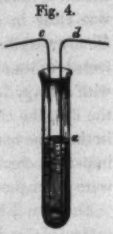
§ 14. *Boiling by an Internal Source of Heat.*

Two large test-tubes were fixed air-tight in the same case. On the 8th of November,

* Kidney has been mentioned by Dr. Bastian as a substance with which he demonstrates the occurrence of spontaneous generation. He does not mention the extraordinary turbidity of the infusion, which proved so troublesome to me.

after the floating matter had subsided, infusions of hay and turnip were introduced. Dipping into each test-tube were two tinned copper wires, connected below by a spiral of platinum wire. The arrangement is represented in fig. 4. The copper wires (*c d*) passed through the case, and were connected with a voltaic battery outside. The spiral was heated by the current. After a few minutes ebullition set in, and was continued for five minutes in each tube. Two other tubes containing the same infusions were boiled in the same way, and afterwards hung on outside the case containing the two protected tubes.

Fig. 4.



In a separate case were placed two tubes containing infusions of beef and mutton. The arrangement and the treatment were precisely the same as those just described in the case of hay and turnip.

Examined some months subsequently, the exposed tubes of all four infusions were found turbid and covered with *Penicillium*, while all the four protected tubes remained unchanged. During the boiling process some flocculi detached themselves from the tinned surfaces of the copper wires; but in the protected tubes these have fallen to the bottom, and left the supernatant liquid clear. Platinum wires would have been better than tinned copper ones.

§ 15. *Partial Discussion of the Results.*

Thus by experiments, reiterated in many cases, with urine, mutton, beef, pork, hay, turnip, tea, coffee, hops, haddock, sole, salmon, codfish, turbot, mullet, herring, eel oyster, whiting, liver, kidney, hare, rabbit, fowl, pheasant, grouse, has the induction been established that the power of developing Bacterial life by atmospheric air, and its power of scattering light, go hand in hand. We shall immediately examine more closely what this means.

In his published works, Dr. Bastian has frequently dwelt upon the necessity of employing strong infusions when investigating the phenomena of spontaneous generation. I would therefore recall to mind what has been stated on a previous page, that in most of the experiments here described the infusion at starting was strong, and that it was permitted to evaporate with extreme slowness until its concentration became three or four fold what it had been at starting. Every experiment was thus converted into an indefinite number of experiments on infusions of different strengths. Never, in my opinion, was the requirement as to concentration more completely fulfilled, and never was the reply of Nature to experiment more definite and satisfactory. The temperatures, moreover, to which the infusions have been subjected embrace those hitherto found effectual, extending indeed beyond them in both directions*. They reached from a lower limit of 50° to a higher limit of more than 100° Fahr. Still higher temperatures were applied in other experiments to be described subsequently. With regard to the number of the infusions, more than fifty moteless chambers, each with its system of tubes, have been tested. There is no shade of uncertainty in any of the results. In every instance we have, within the chamber, perfect limpidity and sweetness—without the chamber, putridity and its

* See Proc. of Roy. Soc. vol. xxi. p. 130, where a temperature of 70° is described as effectual.

characteristic smells. In no instance is the least countenance lent to the notion that an infusion deprived by heat of its inherent life, and placed in contact with air cleansed of its visibly suspended matter, has any power whatever to generate life anew.

If it should be asked how I have assured myself that the protected liquids do not contain *Bacteria*, I would, in the first place, reply that with the most careful microscopic search I have been unable to find them. But much more than this may be affirmed. The electric or the solar beam is a far more powerful and searching test in this matter than the microscope. In the foregoing pages I have more than once described the clearness of my protected infusions, after months of exposure, as equal to that of distilled water. So far is this from being an exaggeration, that it falls short of the truth; for I have never seen distilled water so free from suspended particles as the protected infusions prove themselves to be. When for months a transparent liquid thus defies the scrutiny of the searching beam, maintaining itself free from every speck which could scatter light as a *Bacterium* scatters it—when, moreover, an adjacent infusion, prepared in precisely the same way, but exposed to the ordinary air, becomes first hazy, then turbid, and ends by wholly shattering the concentrated beam into irregularly scattered light, I think we are entitled to conclude that *Bacteria* are as certainly absent from the one as they are present in the other. (See Note I. at the end.)

For the right interpretation of scientific evidence something more than mere sharpness of observation is requisite, very keen sight being perfectly compatible with very weak insight. I was therefore careful to have my infusions inspected by biologists, not only trained in the niceties of the microscope, but versed in all the processes of scientific reasoning. Their conclusion is that it would simply weaken the demonstrative force of the experiments to appeal to the microscope at all.

§ 16. *Suspended Particles in Air and Water; their relation to* Bacteria.

Examined by the concentrated solar rays, or by the condensed electric beam, the floating matter of the air is seen to consist:—first, of particles so coarse that their individual motions can be followed by the eye; secondly, of a finer matter which is not to be distinguished as motes, but which emits a uniform and changeless light. In this finer matter the coarser motes move as in a medium.

As regards the production of colour, the action of small particles has been examined by Brücke in a paper "On the Colours of Turbid Media"*. In relation to the question of polarization, Professor Stokes has made some remarks in his memoir "On the Change of the Refrangibility of Light"†. I may also be permitted to refer to my own papers "On New Chemical Reactions by Light" and "On the Blue Colour of the Sky," in the Proceedings of the Royal Society for 1868–69, and to a paper "On the Action of Rays of High Refrangibility on Gaseous Matter," in the Philosophical Transactions for 1870. M. Soret, Lord Rayleigh, and Mr. Bosanquet have also worked at this subject, which, as far as it now concerns us, a few words will render clear.

* Pogg. Ann. lxxxviii. p. 363.

† Philosophical Transactions, vol. 142, pp. 529–530

When the track of a parallel beam in dusty air is looked at horizontally through a Nicol's prism, in a direction perpendicular to the beam, the longer diagonal of the prism being vertical, a portion of the light from the finer matter, being polarized, is extinguished. The coarser motes, on the other hand, which do not polarize the light, flash out with greater force, because of the increased darkness of the space around them.

The individual particles of the finest floating matter of the air lie probably far beyond the reach of the microscope. At all events it is experimentally demonstrable that there are particles which act similarly upon light, and which are entirely ultra-microscopic. A few days ago, for example, an inverted bell-jar was filled with distilled water, into which, while it was briskly beaten by a glass rod, was dropped a solution of mastic in alcohol. The proportion was less than that employed by Brücke, being about 10 grains of the gum to 1000 grains of the alcohol. The jar was placed under a skylight, at the height of the eye above the floor. It was of a beautiful cerulean hue, this colour arising wholly from the light scattered by the mastic particles. Looked at horizontally through a Nicol's prism, with its shorter diagonal vertical, the blue light passed freely to the eye. Turning the long diagonal vertical, the scattered light was wholly quenched, and the jar appeared as if filled with ordinary pure water.

I tried the effect of a powerful filter upon those particles, and found that they passed sensibly unimpeded through forty layers of the best filtering-paper*.

The liquid containing them was examined by a microscope magnifying 1200 diameters. The suspended mastic particles entirely eluded this power, the medium in which they swam being as uniform as distilled water in which no mastic whatever had been precipitated.

The optical deportment of the floating matter of the air proves it to be composed, in part, of particles of this excessively minute character. The concentrated beam reveals them collectively, long after the microscope has ceased to distinguish them individually. They are, moreover, organic particles, which may be removed from the air by combustion. In presence of such facts, any argument against atmospheric germs, based upon their being beyond the reach of the microscope, loses all validity.

We are here brought face to face with a question of extreme importance, which it will be useful to clear up. "Potential germs" and "hypothetical germs" have been spoken of with scorn, because the evidence of the microscope as to their existence was not forthcoming. Sagacious writers had drawn from their experiments the perfectly legitimate inference that in many cases the germs exist, though the microscope fails to reveal them. Such inferences, however, have been treated as the pure work of the imagination, resting, it was alleged, on no real basis of fact. But in the concentrated beam we possess what is virtually a new instrument, exceeding the microscope indefinitely in power. Directing it upon media which refuse to give the coarser instrument any information as to what they hold in suspension, these media declare themselves to

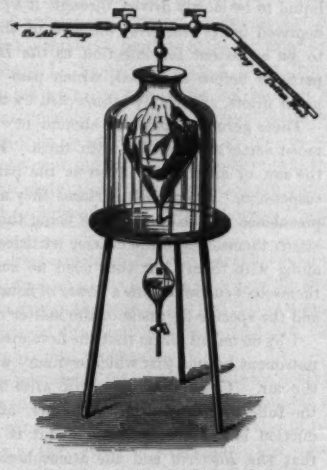
* There are filters, however, which stop them; but of this immediately.

be crowded with particles—not hypothetical, not potential, but actual and myriadfold in number—showing the microscopist that there is a world beyond even his range.

In §§ 6 and 8 experiments on the infection of clear infusions by others containing visible *Bacteria* are referred to. But for the infection to be sure it is not necessary that the *Bacteria* should be visible. Over and over again I have repeated the experiments of Dr. Burdon Sanderson on the infective power of ordinary distilled water, in which the microscope fails to reveal a *Bacterium*. The water, for example, furnished to the Royal-Institution laboratory by Messrs. Hopkin and Williams is sensibly as infectious as an infusion swarming with *Bacteria*.

Perhaps the severest experiment of this kind ever made was one executed by Dr. Sanderson with water prepared by myself. In 1871 I sought anxiously and assiduously for water free from suspended particles. The liquid was obtained in various degrees of purity, but never entirely pure. Knowing the wonderful power of extrusion, as regards foreign matter, brought into play by water in crystallizing, the thought occurred to me of examining the liquid derived from the fusion of the most transparent ice. Mr. Cottrell, at my request, arranged the following apparatus for me:—Through the plate of an air-pump (fig. 5) passed air-tight the shank of a large funnel. A small glass bulb, B, furnished with a glass stopcock, was attached to the shank of the funnel below. Prior to being put together all parts of the apparatus had been scrupulously cleansed. In the funnel was placed a block of ice, I, selected for its transparency, having a volume of 1000 cubic inches or thereabouts, and over the ice was placed an air-tight receiver. Several times in succession the air was removed from this receiver, its place on each occasion being taken by other air carefully filtered through cotton-wool. The transparent ice was thus surrounded by moteless air.

Fig. 5.



The ice was now permitted to melt; its water trickled into the small glass bulb below, which was filled and emptied a great number of times. From the very heart of the block of ice the water was finally taken and subjected to the scrutiny of the concentrated beam. It proved to be the purest liquid I had ever seen—probably the purest human eye had ever seen; but still it contained myriads of ultra-microscopic particles. The track of the beam through it was of the most delicate blue, the blue light being perfectly polarized. It could be wholly quenched by a Nicol's prism, the beam then

passing through the liquid as through a vacuum. A comparison of the light with that scattered by such mastic particles as those above referred to, proved the suspended particles of the ice-water to be far smaller than those of the mastic. No microscope, therefore, could come near them*. Such water, however, was proved by Dr. SANDERSON to be as infectious as the water from any ordinary tap.

Infinitesimal as these particles are, however, they may be separated by mechanical means from the liquid in which they are held in suspension. Filters of porous earthenware, such as the porous cells of BUNSEN's battery, have been turned to important account in the researches of Dr. ZAHN, Professor KLEBS, and Dr. BURDON SANDERSON. In various instances it has been proved that, as regards the infection of living animals, the porous earthenware intercepts the contagium. For the living animal, organic infusions or PASTEUR's solution may be substituted. Not only are ice-water, distilled water, and tap-water thus deprived of their powers of infection, but, by plunging the porous cell into an infusion swarming with Bacterial life, exhausting the cell, and permitting the liquid to be slowly driven through it by atmospheric pressure, the filtrate is not only deprived of its *Bacteria*, but also of those ultra-microscopic particles which appear to be as potent for infection as the *Bacteria* themselves. The precipitated mastic particles before described, which pass unimpeded through an indefinite number of paper filters, are wholly intercepted by the porous cell.

These germinal particles abound in every pool, stream, and river. All parts of the moist earth are crowded with them. Every wetted surface which has been dried by the sun or air contains upon it the particles which the unevaporated liquid held in suspension. From such surfaces they are detached and wafted away, their universal prevalence in the atmosphere being thus accounted for. Doubtless they sometimes attach themselves to the coarser particles, organic and inorganic, which are left behind along with them; but they need no such rafts to carry them through the air, being themselves endowed with a power of flotation commensurate with their extreme smallness and the specific lightness of the matter of which they are composed.

I by no means affirm that the developed *Bacterium*, which requires for its maintenance nutriment beyond that which ordinary water can always supply, is never wafted through the air. Cases doubtless will arise favourable for the growth and dispersion of the full-grown organism. Whether, after desiccation, it retains the power of reproduction is another question. But it ought, I think, to be steadily borne in mind that the *Bacteria* and the atmospheric matter from which they are developed are, in general, different things. I have carefully sought for atmospheric *Bacteria*, but have never found them. They have never, to my knowledge, been found by others; and that they arise from matter which has not yet assumed the Bacterial form is, as just shown, capable of demonstration. An organic infusion, boiled and shielded from atmospheric particles, will remain clear for an indefinite period, while a fragment of glass which

* I have endeavoured to convey some notion of the smallness of these scattering particles in 'Fragments of Science,' 1876, pp. 441–443. See note on Mr. DALLINGER's observations at the end of this Memoir.

has been exposed to the air, but on which no trace of a *Bacterium* is to be found, will in two or three days develop in it a multitudinous crop of life.

We have now to look a little more closely at these particles, foreign to the atmosphere but floating in it, and proved beyond doubt to be the origin of all the Bacterial life which our experiments have thus far revealed. We must also look at them as they exist in water, in countless multitudes, being as foreign to this medium as the floating atmospheric dust is to the air in which it swims. The existence of the particles is quite as certain as if they could be felt between the fingers, or seen by the naked eye. Supposing them to augment in magnitude until they come, not only within range of the microscope, but within range of the unaided senses. Let it be assumed that our knowledge of them under these circumstances remains as defective as it is now—that we do not know whether they are germs, particles of dead organic dust, or particles of mineral matter. Suppose a vessel (say a flower-pot) to be at hand filled with nutritious earth, with which we mix our unknown particles, and that in forty-eight hours subsequently buds and blades of well-defined cresses and grasses appear above the soil. Suppose the experiment when repeated a hundred times to yield the same unvarying result. What would be our conclusion? Should we regard those living plants as the product of dead dust, of mineral particles? or should we regard them as the offspring of living seeds? The reply is unavoidable. We should undoubtedly consider the experiment with the flower-pot as clearing up our preexisting ignorance; we should regard the fact of their producing cresses and grasses as proof positive that the particles sown in the earth of the pot were the seeds of the plants which have grown from them. It would be simply monstrous to conclude that they had been "spontaneously generated."

This reasoning applies word for word to the development of *Bacteria* from that floating matter which the electric beam reveals in the air, and in the absence of which no Bacterial life has been generated. I cannot see a flaw in the reasoning; and it is so simple as to render it unlikely that the notion of Bacterial life developed from dead dust can ever gain currency among the members of the medical profession.

It has been said of those whom the evidence adduced in favour of spontaneous generation fails to convince, that they seem willing to believe in almost any infringement of natural uniformity rather than admit the doctrine*. This surely is an inversion of the true order of the facts. Natural uniformity is the record of experience; and, apart from the phenomena to be accounted for, there is not a vestige of experience, possessed either by the man of science or the human race, which warrants the notion that dead dust, and not living seed, is the source of the crops which spring from our infusions after their impregnation by the floating particles of the atmosphere.

* Transactions of the Pathological Society, vol. xxvi. p. 273.

§ 17. *Dr.* Bastian's *Experiments.*

The uniform sterility of the boiled infusions described in the foregoing pages, when protected from the floating matter of the air, proves that they do not contain germs capable of generating life. Dr. Bastian, indeed, affirms that a temperature of 140° Fahr. reduces, in all cases, such germs to a state of actual or potential death. But even in flasks which have been raised to a temperature of 212°, and hermetically sealed, putrefaction, and its associated Bacterial life, do, he alleges, most certainly arise; from which he infers that *Bacteria* are spontaneously generated. "We know," he says, "that boiled turnip- or hay-infusions, exposed to ordinary air, exposed to filtered air, to calcined air, or shut off altogether from contact with air, are more or less prone to swarm with *Bacteria* and *Vibriones* in the course of from two to six days" *.

We are here met by a difficulty at the outset. Dr. Bastian's proof of Bacterial death at 140° Fahr. consists solely in the observed fact, that when a certain liquid is heated to that temperature no life appears in it afterwards. In another liquid, however, he finds that life appears two days after it has been heated to 212°. Instead of concluding logically that in the one liquid life is destroyed and in the other not, he chooses to assume arbitrarily that 140° Fahr. is the death-temperature for both; and this being so, the life observed in the second liquid figures, in his inference, as a case of spontaneous generation. A great deal of Dr. Bastian's most cogent reasoning rests upon this extraordinary foundation. Assumptions of this kind guide him in his most serious experiments. He finds, for example, that a mineral solution does not develop *Bacteria* when exposed to the air; and he concludes from this that an organic infusion also may be thus exposed without danger of infection. He exposes turnip-juice accordingly, obtains a crop of *Bacteria*, which, in the light of his assumption, are spontaneously generated. Such are the warp and woof of some of the weightiest arguments on this question which have been addressed by him to the Royal Society †.

Granting, then, all that Dr. Bastian alleges regarding his experiments to be correct, the logical inference would be very different from his inference. But are his statements correct? This is the really important point; and to its examination I now address myself.

§ 18. *Experiments with Filtered Air.*

A bell-jar containing about 700 cubic inches of air was firmly cemented to a slab of wood supported on three legs ‡. Through the slab passed, air-tight, three large test-

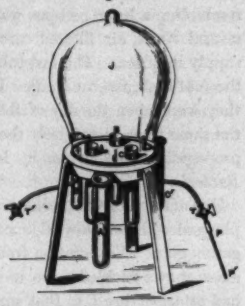
* Evolution and the Origin of Life, p. 94.

† Proceedings, vol. xxi. p. 130.

‡ Two hoops of sheet iron, with an annular space about an inch wide, were fastened on to the slab of wood. The annular space was filled with hot cement, into which the hot bell-jar was pressed. The circular space within the smaller hoop was also covered by a layer of cement.

tubes (A, B, C, fig. 6). Prior to cementing, the tubes had been three fourths filled, one with an infusion of hay, another with an infusion of turnip, and a third with an infusion of mutton. On the 2nd of November the mote-laden air was pumped out, air slowly filtered through a long tight plug of cotton-wool being allowed to take its place. The jar was emptied and refilled until the closest scrutiny by a concentrated beam revealed no floating matter within it. The infusions were then boiled for five minutes, and abandoned to the air of the jar. During ebullition a small quantity of the liquid in one of the tubes boiled over, and rested upon the interior resinous surface at a little distance from the mouths of two of the tubes. The germinal matter, it may be remarked, is not readily blown away from such a surface, and it certainly was not removed by our feeble current of filtered air. Three similar tubes containing the same infusion were placed at the same time beside the protected ones.

Fig. 6.



In three days these exposed tubes became turbid and charged with life; *but for three weeks the infusions in contact with the filtered air remained perfectly clear.*

At the end of three weeks, that is on the 23rd of November, I desired my assistant to renew the air in the bell-jar. He pumped it out, and while permitting fresh air to enter through the cotton-wool filter, my attention was directed to a couple of small round patches of *Penicillium* resting on the liquid that had boiled over. I at once made the remark that the experiment was a dangerous one, as the entering air would probably detach some of the spores of the *Penicillium* and diffuse them in the bell-jar. This was, therefore, filled very slowly, so as to render the disturbance a minimum. Next day, however, a tuft of mycelium was observed at the bottom of one of the three tubes, namely that containing the hay-infusion. It has by this time grown so as to fill a large portion of the tube. For nearly a month longer the two tubes containing the turnip- and mutton-infusions maintained their transparency unimpaired. Late in December the mutton-infusion, which was in dangerous proximity to the outer mould, showed a tuft of *Penicillium* upon its surface. The beef-infusion continued bright and clear for nearly a fortnight longer. The cold winter weather caused me to add a third gas-stove to the two which had previously warmed the room where the experiments are conducted. The warmth of this stove played upon one side of the bell-jar; and on the day after the lighting of the stove, the beef-infusion gave birth to a tuft of mycelium. In this case the small spots of *Penicillium* might have readily escaped attention; and had they done so we should have had here three cases of "spontaneous generation" far more striking than many that have been adduced.

The experiment was subsequently made upon a larger scale. Twelve very large test-tubes were caused to pass air-tight through a slab of wood; the wood was thickly coated

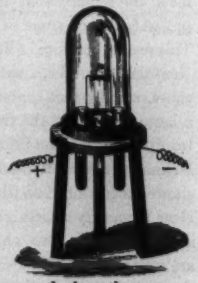
with cement, in which, while it was hot and soft, a heated "propagating-glass," resembling a huge bell-jar, was imbedded. The air within the glass was pumped out several times, air filtered carefully through a plug of cotton-wool being permitted to supply its place. The test-tubes contained infusions of hay, turnip, beef, and mutton, three of each, twelve in all. For two months they remained as clear and cloudless as they were upon the day of their introduction, while twelve similar tubes, prepared at the same time, in precisely the same way, and hung on to the slab of wood outside the propagating-glass, were, in less than a week, clogged with mycelium, mould, and *Bacteria*.

One of the protected tubes was accidentally broken, and though its aperture was rapidly plugged with cotton-wool, some common air must, at the time, have entered the propagating-glass. Evaporation from the infusions went on; the vapour was condensed by the glass above, trickled down its interior surface, carrying with it, in part, such matter as had attached itself to that surface. A kind of pool was thus formed upon the cement below. This, after an interval of three months, is now spotted with disks of *Penicillium*, by the spores of which one or two of the infusions have been recently invaded, the production of very beautiful mycelium-tufts being the consequence.

§ 19. *Experiments with Calcined Air.*

Six years ago* I showed that the floating matter of London air could be completely removed by permitting a platinum wire heated to whiteness to act upon it for a sufficient time. I availed myself of this mode of calcining the air on the present occasion. The apparatus employed is shown in fig. 7. A glass shade, S, is placed upon a slab of wood mounted on a tripod, and through which passes three large test-tubes nearly filled with the infusion to be examined. A platinum spiral, *p*, unites the ends of two upright copper wires, which pass through the stand and are seen coiled outside it. The shade is surrounded by a tin collar, with a space of about half an inch all round between it and the shade. This space is filled with cotton-wool firmly packed. Connecting the wires with a battery of fifteen cells, the spiral *p* was raised to whiteness, and was permitted to continue so for five minutes. Experiments previously executed had shown that this sufficed for the entire removal of the floating matter. When the spiral was heated, a portion of the expanded air was driven through the cotton-wool packing below; and when the current was interrupted, this air, returning into the shade, was prevented by the cotton-wool from carrying any floating matter with it.

Fig. 7.



The first three substances brought into contact with air calcined in this way were damson-juice, pear-juice, and infusion of yeast. They were boiled for five minutes, and

* Proc. Roy. Inst. vol. vi. pp. 4 & 5.

for five months they have remained without speck or turbidity. Other tubes similarly boiled, and placed underneath shades containing the floating matter of the air, have long since fallen into mould and rottenness.

Turnip- and hay-infusions rendered slightly alkaline have been mentioned as particularly prone to spontaneous generation. I wished to test this. On the 26th of November, therefore, four shades were prepared, two containing strong turnip-infusion and hay-infusion unneutralized, two containing infusions which had been rendered slightly superneutralized by caustic potash. The alleged spontaneous development of life was not observed. The tubes exhibit to this hour the clearness and colour which they showed on the day they were boiled. Hermetically sealed tubes, containing the same infusions, prepared on the same day, remain equally clear; while the specimens exposed to the laboratory air have fallen into rottenness.

The experiments with calcined air were also executed in another form and on a larger scale. A "propagating-glass," similar to that already described, was cemented in the same way to a slab of wood through which passed twelve large test-tubes. The infusions, as before, were hay, turnip, beef, and mutton. The air being removed from the propagating-glass by a good air-pump, its place was supplied by other air which had passed slowly through a red-hot platinum tube containing a roll of platinum gauze, also heated to redness. Tested by a searching beam, this calcined air was found quite free from floating matter. For two months no speck invaded the limpidity of the infusions exposed to it, while a week's exposure to the ordinary air sufficed to reduce twelve similar infusions, hung on to the slab of wood outside the glass, to rottenness.

§ 20. *Infusions withdrawn from Air.*

The arrangement was the same as that in the first experiment with filtered air, the only difference being that the bell-jar, with a view to its more perfect exhaustion, was smaller. It was cemented air-tight to a slab of wood through which passed three large test-tubes, filled to about two thirds of their capacity with infusions of beef, mutton, and turnip respectively. The air was pumped out six times in succession, and filled after each exhaustion with air carefully filtered through cotton-wool. While this air was in contact with the infusions they were boiled in a brine-bath. The receiver was afterwards exhausted as perfectly as a good air-pump could exhaust it; while outside the receiver were hung three tubes to compare with those within.

Here the protected infusions remained as clear as they were on the day of their introduction, not only after the exposed infusions had charged themselves with life, but for many weeks after they had evaporated away.

Such, then, are the tests to which I have subjected the statement that "boiled turnip- and hay-infusions exposed to filtered air, to calcined air, or shut off altogether from contact with air, are more or less prone to swarm with *Bacteria* and *Vibriones* in

the course of from two to six days." In no single instance has the statement borne the stress of accurate experiment. These results, and others that might be adduced, leave no doubt upon my mind that the deportment of air from which the floating matter has been removed by filtration or calcination is precisely the same as that of air from which the particles have disappeared by self-subsidence.

§ 21. *The Germ-theory of Contagious Disease.*

It is in connexion with the so-called germ-theory of contagious disease that the doctrine of spontaneous generation assumes its gravest aspect. My interest in the general question was first excited by the imperishable investigations of PASTEUR, while the medical bearings of the doctrine were subsequently made clear to me, mainly, I ought to say, by the writings and conversation of Dr. WILLIAM BUDD, who was the first of our countrymen to grasp definitely the doctrine of "the vitality of contagia," which is now every day gaining ground.

At the present moment, indeed, no other medical principle occupies so much thought, or is the subject of so much discussion. "How does it happen," says Dr. BURDON SANDERSON*, "that these *Bacteria*, which we suppose must have existed half a dozen years ago in as great numbers as at present, were then scarcely heard of, and that they now occupy so large a place in the medical literature of this country and of Germany, and have lately afforded material for lively discussion in the French Academy?" Dr. SANDERSON points out the relation of LISTER in England, and of HALLIER in Germany, to the movement regarding *Bacteria* which is now working like a ferment through the medical world. But to no other workers in this field are we more indebted than to Dr. SANDERSON himself, and to his colleagues, for the continued and successful prosecution of researches bearing upon the pathology of contagion.

"In 1870," writes Mr. JOHN SIMON, in one of his excellent reports to the Privy Council, "I had the honour of presenting Dr. SANDERSON'S first report of researches made in this matter. At that time general conclusions seemed justified, first, that the characteristic-shaped elements which the microscope had shown abounding in various infective products are self-multiplying organic forms, not congeneric with the animal body in which they are found, but apparently of the lowest vegetable kind; and secondly, that such living organisms are probably the essence, or an inseparable part of the essence, of all contagia of disease. . . . . This view of the matter has since then become greatly more distinct, in consequence of the investigations made by Dr. SANDERSON, particularly in 1871 and 1872, with reference to the common septic contagium or ferment. For in that ferment there seems now to be identified a force which, acting disintegratively upon organic matter, whether dead or living, can, on the one hand, initiate putrefaction of what is dead, and, on the other hand, initiate febrile and inflammatory processes in what is living."

* British Medical Journal, January 16, 1875.

The latest investigation of Dr. KLEIN has reference to the intimate anatomy of enteric fever. Its distinctive feature is set forth in the following extract from the report upon it by Mr. SIMON:—"The paper has its distinctive and very great interest in the fact that it purports to describe for the first time the contagium of enteric fever as something cognizable to the eye; in respect of certain multiplying microscopical forms, apparently of the lowest vegetable life, which are found in innumerable swarms in the bowel-textures and bowel-discharges of the sick; penetrating from the former to diffuse throughout the patient's general system*, and teeming in the latter to represent, as this view supposes, the possible germs of epidemic infection."

As regards the medical profession, results like the foregoing and the interpretations affixed to them, are simply revolutionary. They are, therefore, not likely to be accepted without opposition. At a Meeting of the Pathological Society, held on the 6th of last April, the germ-theory of disease was formally introduced as a subject for discussion, the debate being continued with great ability and earnestness at subsequent meetings. The Conference was attended by many distinguished medical men, some of whom were profoundly influenced by the arguments, and none of whom disputed the facts brought forward against the theory on that occasion. The leader of the debate, and the most prominent speaker, was Dr. BASTIAN, to whom also fell the task of replying on all the questions raised. The coexistence of *Bacteria* and contagious disease was admitted; but instead of considering these organisms as "probably the essence, or an inseparable part of the essence" of the contagium, Dr. BASTIAN contended that they were "pathological products," spontaneously generated in the body after it had been rendered diseased by the real contagium. The grouping of the ultimate particles of matter to form living organisms, Dr. BASTIAN considers to be an operation as little requiring the action of antecedent life as their grouping to form any of the "other less complex chemical compounds." Such a position must, of course, stand or fall by the evidence which its supporter is able to produce; and accordingly Dr. BASTIAN appeals to the law and testimony of experiment as demonstrating the soundness of his view. He seems quite aware of the gravity of the matter in hand: this is his deliberate and almost solemn appeal:—"With the view of settling these questions, therefore, we may carefully prepare an infusion from some animal tissue, be it muscle, kidney, or liver; we may place it in a flask whose neck is drawn out and narrowed in the blowpipe-flame, we may boil the fluid, seal the vessel during ebullition, and keeping it in a warm place, may await the result, as I have often done. After a variable time the previously heated fluid within the hermetically sealed flask swarms more or less plentifully with *Bacteria* and allied organisms—even though

* In the silkworm epidemic called *pébrine*, which was extirpated by PASTEUR, the parasitic contagium first took possession of the intestinal canal, and spread thence "throughout the patient's general system." He would be a hardy man who would deny the identity of parasite and contagium in this case, which appears to be precisely analogous to that of typhoid fever. See 'Fragments of Science,' 1876, pp. 135–139.

the fluids have been so much degraded in quality by exposure to the temperature of 212° Fahr., and have thereby, in all probability, been rendered far less prone to engender independent living units than the unheated fluids in the tissues would be" *.

We have here, to use the words of Dr. Bastian, "a question lying at the root of the pathology of the most important and most fatal class of diseases to which the human race is liable." Let us now examine his settlement of the question, as described in the foregoing extract by himself.

§ 22. *Experiments with Hermetically sealed Vessels.*

Experiments with hermetically sealed tubes were begun on the 5th of October. The shape of the tubes after sealing is represented in fig. 8. Each of them contained about an ounce of liquid. They were boiled for only three minutes in an oil-bath, and were sealed, during ebullition, not by a blowpipe, but by the far more effectual spirit-lamp flame.

Fig. 8.

Hay.—Four tubes were charged on the date mentioned with a strong infusion, four with a weak infusion. All eight flasks remain to the present hour clear.

Turnip.—Two kinds of turnip were tried in these first experiments. Two tubes were charged with a strong infusion, and two with a weak infusion of a sound hard turnip; while two other pairs of tubes were filled with strong and weak infusions from a soft woolly turnip. All the tubes remain transparent to the present time. Two or three days' exposure to the air of the laboratory sufficed to cloud all these infusions and fill them with life.

On the 8th of October twenty-one tubes were charged with infusions of the following substances:—Mackerel, beef, eel, oyster, oatmeal, malt, potato. There were three tubes of each infusion. All of them remain to the present hour unchanged.

I had not previously seen a more beautiful illustration of the dichroitic action which produces the colours of the sky than in the case of the oyster-infusion. With reflected light it presented a beautiful cerulean hue, while it was yellow by transmitted light. This was due to the action of suspended particles which defied the power alike of ordinary filtration and of the microscope. At right angles to a transmitted beam the infusion copiously discharged perfectly polarized light. Suspended particles in the potato-infusion produced a somewhat similar effect, but it was by no means so fine as that of the oyster-infusion. By ordinary filtration it was not possible completely to rid the malt and oatmeal of suspended matter; but both remain exactly as they were when the flasks containing them were sealed.

These experiments had been made before the volume of the Transactions of the Pathological Society containing the discussion referred to above came into my hands†.

* Transactions of the Pathological Society of London, 1875, p. 272.

† To the courtesy of Dr. Bastian I am indebted for a separate copy of the report of the discussion here referred to.

It caused me to turn again to my tubes, seeking further evidence. On the 12th of November thirty-six of them were charged, boiled, and hermetically sealed; on the 13th fifty-seven, on the 16th thirty-one, and on the 17th six tubes were similarly treated. The entire group of tubes, therefore, numbered one hundred and thirty. I tried moreover to multiply the chances of spontaneous generation by making the infusions of the most diverse materials. The following Table gives the names of the substances operated on, the number of tubes sealed, and the date of sealing:—

Fowl	6 tubes.	November 12th.
Mutton	6 „	„
Wild Duck	6 „	„
Beef	6 „	„
Herring	6 „	„
Haddock	6 „	„
Mullet	6 „	November 13th.
Codfish	6 „	„
Pheasant	6 „	„
Heart	6 „	„
Rabbit	6 „	„
Hare	6 „	„
Snipe	6 „	„
Partridge	6 „	„
Plover	5 „	„
Liver	4 „	„
Tongue of Sheep	6 „	November 16th.
Brains of Sheep	3 „	„
Sweetbread	6 „	„
Humour of Ox-eye (undiluted)	2 „	„
Lens of Ox-eye	3 „	„
Lungs of Sheep	5 „	„
Tripe	6 „	„
Sole	6 „	November 17th.

The tubes were immersed in groups of six at a time in an oil-bath, boiled for three minutes, and then sealed.

More than one hundred of these flasks were sensibly transparent and free from turbidity at the outset, and they remain so to the present hour. In some cases, however, it was not possible to wholly remove turbidity by filtration. I have already referred to the opalescence of oyster-infusion, which has invariably appeared whenever oyster has been digested. A still more pronounced case of the kind is furnished by an infusion of the crystalline lens of the ox. Nothing hitherto encountered imitates

the flush of the true opal so closely as this infusion. Filtration through 100 layers of paper was quite incompetent to remove the suspended particles to which this opalescence is due. Some of the other infusions remained turbid under filtration, without exhibiting what I should call opalescence. The sheep's lungs furnish an example of this. In some cases, moreover, where repeated filtering failed to remove the suspended particles, a few weeks' quiet caused them to sink, and leave the supernatant liquid clear. It may be worth remarking that some rabbit-infusions have shown a decided opalescence, while others have been perfectly clear. The same remark applies to turnip-infusions, some of which have been found as clear as distilled water, while in general a slight opalescence is not to be got rid of by filtering.

These later experiments are quite in harmony with the earlier ones. Not one of this cloud of witnesses testifies in favour of Dr. Bastian. Not a single flask of the multitude manifests the deportment alleged by him to be a matter of common observation. If the power of spontaneous generation be a scientific verity, surely amid opportunities so multiplied and various it must have asserted itself. That the infusions employed were not "degraded" by the boiling so as to be incapable of supporting life, was proved by the fact that exposed tubes containing the same infusions, treated in precisely the same way, resolved themselves with the usual speed into Bacterial swarms. The conclusion to which these results point is, that here, as elsewhere, Dr. Bastian has allowed the gravest errors to invade his experimental work.

§ 23. *Conditions as to the Temperature and Strength of Infusions.*

In connexion with these experiments, I have sought, to the best of my ability, to meet every condition and requirement laid down by others as essential to success. With regard to warmth, a temperature of 90° was generally attainable in our laboratory, while on certain days of mild weather without, and in favourable positions within, the temperature to which the infusions were subjected reached over 100° Fahr. As Dr. Bastian, however, has recently laid considerable stress on warmth, though most of his results were obtained with temperatures from 15° to 30° lower than mine*, I thought it desirable to meet this new requirement also. The sealed tubes, which had proved barren in the Royal Institution, were suspended in boxes copiously perforated, so as to permit of the free circulation of warm air, and placed under the supervision of an intelligent assistant in the Turkish Bath in Jermyn Street. The washing-room of the establishment was found to be particularly suitable for our purpose; and here, accordingly, the boxes were suspended. From two to six days are allowed by Dr. Bastian for the generation of organisms in hermetically sealed tubes. Mine remained in the washing-room for nine days. Thermometers placed in the boxes, and read off twice or three times a day, showed the temperature to vary from a minimum of 101° to a maximum of 112° Fahr. At the end of nine days the infusions were as clear as at the beginning.

* Proc. Roy. Soc. vol. xxi. p. 130. Also 'Beginnings of Life,' vol. i. p. 354.

They were then removed to another position where the temperature was a few degrees higher. Dr. BASTIAN mentions 115° as favourable to spontaneous generation. For fourteen days the temperature hovered about this point, falling once as low as 106°, reaching 116° on three occasions, 118° on one, and 119° on two. The result was quite the same as that recorded a moment ago. The higher temperatures proved perfectly incompetent to develop life*.

Fifty-six observations, including both the maximum and minimum thermometers, were taken while the tubes occupied their first position in the washing-room, and seventy-four while they occupied the second position. The whole record, carefully drawn out, is before me, but I trust the statement of the major and minor limits of temperature will suffice.

Dr. BASTIAN'S demand for these high temperatures is, as already remarked, quite recent. Prior to my communication to the Royal Society on January 13, he had successfully worked with temperatures lower than those within my reach in Albemarle Street. There I followed his directions, adhered strictly to his prescriptions; but, taking care to boil and seal the liquids aright, his results refused to appear in my experiments. On learning this he raised an objection as to temperature, and made a new demand. With this I have complied; but his position is unimproved.

With regard to the question of concentration, I have already referred, in sections 3 and 16 of this memoir, to the great diversity in this particular presented by all my infusions, through their slow evaporation. But more than a general conformity to prescribed conditions was observed here also. The strength of an infusion is regarded as fixed by its specific gravity; and I have worked with infusions of precisely the same specific gravity as those employed by Dr. BASTIAN. This I was specially careful to do in relation to the experiments described and vouched for, I fear incautiously, by Dr. BURDON SANDERSON in vol. vii. p. 180 of 'Nature.' It will there be seen that though failure attended some of his efforts, Dr. BASTIAN did satisfy Dr. SANDERSON that in boiled and hermetically sealed flasks *Bacteria* sometimes appear in swarms. With purely liquid infusions I have vainly sought to reproduce the evidence which convinced Dr. SANDERSON. Hay- and turnip-infusions, of accurately the same character and strength as those employed on the occasion referred to, were prepared, boiled in an oil-bath, carefully sealed up, and subjected to the proper temperatures. In multiplied experiments they remained uniformly sterile. I am therefore compelled to conclude that Dr. SANDERSON has lent the authority of his name to results whose antecedents he had not sufficiently examined, and that the life to which he testifies, in the case of the purely liquid infusions, arose from errors of manipulation.

* My thanks are due to the managers of the bath for their obliging kindness in this matter.

§ 24. *Developmental Power of Infusions and Solutions: Air-germs contrasted with Water-germs.*

Wishing to make no experiment, whether with self-cleansed, filtered, or calcined air, or with infusions withdrawn from air by the air-pump, or contained in hermetically sealed vessels, without exposing the same infusions to ordinary air, this comparison was instituted on the present occasion. One hundred test-tubes, an inch wide and 3 inches deep, were divided into groups, each being filled with the same infusion. The groups were sufficiently numerous to embrace all the substances mentioned in the last Table. Exposed to the uncleansed air, they were attacked with different degrees of rapidity and vigour; but in a few days all of them without exception became muddy and crowded with life. On the whole, the hare- and pheasant-infusions presented the greatest contrast. The tubes containing the former were far gone before those containing the latter were sensibly invaded. The putrescibility of the pheasant, moreover, was exceeded by that of the snipe, partridge, and plover. The sheep's heart examined was also slow to putrefy. A single illustration of this difference of developmental power may be given here.

On the 13th of November thirty tubes, containing infusions of partridge, pheasant, snipe, hare, sheep's heart, and codfish, five tubes being devoted to each, together with four tubes of plover, three of mullet, and three of liver, were exposed to the laboratory air. On the 15th, 16th, and 22nd the numbers taken possession of by *Bacteria* were as follows:—

	15th.	16th.	22nd.
Partridge	0	3	all
Pheasant	0	1	,,
Snipe	2	3	,,
Hare	2	4	,,
Heart	0	1	,,
Codfish	2	4	,,
Plover	1	2	,,
Mullet	1	2	,,
Liver	1	3	,,

They had probably all given way some days before the 22nd, but I had not taken the precaution to look at them.

Thus, then, the first two days produced no visible change in the pheasant-infusion, while in two of the hare-tubes putrefaction had vigorously set in. Three days' exposure caused only one of the pheasant-tubes to yield; four of the hare-infusion had yielded in the same time. The difference between them was also illustrated by the mould upon their surfaces. Some days after their exposure four of the five pheasant-tubes were thickly covered with *Penicillium*, while the five hare-tubes, with one exception, which could hardly be considered such, had repelled the enemy, maintaining their *Bacteria* undisturbed.

Still the deportment of the hare-infusion may have been due, not to any specific difference between hare and pheasant, but to the circumstances preceding death. The researches of Dr. Brown-Séquard show that even the same animal tissue exhibits, under different circumstances, very different tendencies to putrefaction. In guinea-pigs subjected immediately after death to the action of the magneto-electric current, he found the rapidity of putrefaction to correspond with the violence of the tetanization. He also draws attention to the influence of muscular exercise on cadaveric rigidity and putrefaction, showing how quickly they appear in "overdriven cattle and in animals hunted to death." It is known, indeed, to sportsmen that a shot hare will remain soft and limp for a day, while a hunted one becomes rigid in an hour or two. In September 1851 two sheep which had been overdriven to reach a fair were killed by the section of the carotid arteries. "Putrefaction," says Dr. Brown-Séquard, "was manifest before the end of the day, or in less than eight hours after death"*. The deportment of the hare operated upon by me may therefore depend upon the circumstance of its being brought down by the greyhound instead of the gun. It will be interesting to inquire how far the peculiarity of the animal tissue is transferred to the infusion. This is a subject for further investigation†.

Such observations inculcate caution in drawing inferences from the deportment of any infusion as to the distribution of germs in the air. The germs may be demonstrably present while the infusion may not favour their development. As to the quantity of atmospheric germs, the hare and the pheasant might lead to different conclusions. A passing reference to an important practical inference may be fitly introduced here. In one of the earliest of the able series of researches with which he has enriched medical science, Dr. Burdon Sanderson exposed to the air "Pasteur's solution," which is capable of vigorously developing and nourishing *Bacteria* when they are communicated to it by inoculation; he also permitted air to bubble through the liquid, and finding no development in either case he inferred the entire absence of *Bacteria* and their germs from the air, considering water to be their exclusive habitation. Other distinguished men have come to the same conclusion; while in his books and papers, and in the discussion before the Pathological Society already referred to, Dr. Bastian has forcibly dwelt upon the result as justifying the interpretation which he has affixed to his experiments. If, he rightly urges, the air be "entirely free" from matter which could produce *Bacteria*, then their appearance in boiled infusions exposed to the air must be due, not to any thing contained in the air, but to the inherent power of the infusions. Spontaneous generation is undoubtedly the logical outcome of the position that "the germinal manner from which

* Croonian Lecture, Proc. Roy. Soc. 1862, vol. xi. p. 210.

† Five and twenty flasks containing pheasant-infusion were compared during the month of December with five and twenty containing infusion of hare. Neither in the rapidity of Bacterial development, nor in the readiness to support the growth of *Penicillium*, did the considerable differences between hare and pheasant first observed repeat themselves.

Bacteria spring does not exist in ordinary air." The experiments, however, recorded in this memoir constitute an ocular demonstration of the respective parts played by the infusion and the air. A pinch of fungus-spores, taken between the fingers, sown in a suitable medium, and producing their appropriate crop, could not more clearly indicate the origin of that crop than experiments with the luminous beam indicate the origin of our harvests of *Bacteria*. Dr. SANDERSON is, I doubt not, now well aware that his first statement was founded on an error of interpretation. In a lecture delivered at Owens College, Manchester, and published in the 'British Medical Journal' for January 16, 1875, he to a great extent qualifies and corrects his first inference. He there says that the *Bacteria* "attach themselves without doubt to these minute particles, which, scarcely visible in ordinary light, appear as motes in the sunbeam, or in the beam of an electric lamp." In fact the experiments on which he based his first inference owed their barrenness, not to the absence of *Bacteria*-germs from the air, but to the inability or, rather, slowness of his mineral solution to develop them.

With regard to the part played by the visible motes, I may repeat here what has been previously stated, namely, that while the coarser particles could hardly exist in their midst without loading themselves to some extent with the minute germs of *Bacteria*, there is no reason to think the motes indispensable for the diffusion of the germs. Whether they are attached to each other or not, the dryness and the moisture of the air are shared equally by both. The germs, moreover, float in the air more readily than the larger particles; and they, I doubt not, when properly illuminated, shed forth a portion of that changeless light to which reference has been already made, and the perfect polarization of which declares the smallness of the masses which scatter it.

The prevalence of the germinal matter of *Bacteria* in water has been demonstrated by the experiments of Dr. BURDON SANDERSON. But the germs in water, it ought to be remembered, are in a very different condition, as regards readiness for development, from those in air. In water they are already wetted, and ready, under the proper conditions, to pass rapidly into the finished organism. In air they are more or less desiccated, and require a period of preparation more or less long to bring them up to the starting-point of the water-germs*. The rapidity of development in an infusion infected by either a speck of liquid containing *Bacteria* or a drop of distilled water is extraordinary. On the 4th of January I dipped a thread of glass almost as fine as a hair into a cloudy turnip-infusion, and introduced the tip only of the glass fibre into a large test-tube containing an infusion of red mullet: twelve hours subsequently the perfectly pellucid liquid was cloudy throughout. A second test-tube containing the same

* The process by which an atmospheric germ is wetted would be an interesting subject of investigation. A dry microscope covering-glass may be caused to float on water for a year. A sewing-needle may be similarly kept floating, though its specific gravity is nearly eight times that of water. Were it not for some specific relation between the matter of the germ and that of the liquid into which it falls, wetting would be simply impossible. Antecedent to all development there must be an interchange of matter between the germ and its environment; and this interchange must obviously depend upon the character of the encompassing liquid.

infusion was infected with a single drop of the distilled water furnished by Messrs. Hopkin and Williams; twelve hours also sufficed to cloud the infusion thus treated. Precisely the same experiments were made with herring with the same result. In the winter season several days' exposure to warmed air are needed to produce this effect. On the 31st of December a strong turnip-infusion was prepared by digesting in distilled water at a temperature of 120° Fahr. It was divided between four large test-tubes, in one of which the infusion was left unboiled, in another boiled for five minutes, and in the two remaining ones boiled, and after cooling infected with one drop of beef-infusion containing *Bacteria*. In twenty-four hours the unboiled tube and the two infected ones were cloudy, the unboiled tube being the most turbid of the three. The infusion in the unboiled tube was peculiarly limpid after digestion; for turnip it was quite exceptional, and no amount of searching with the microscope could reveal in it at first the trace of a living *Bacterium*; still germs were there which, suitably nourished, passed in a single day into Bacterial swarms without number. Five days failed to produce an effect approximately equal to this in the uninfected boiled tube, which was exposed to the common laboratory air.

There cannot, I think, be a doubt that the germs in the air differ widely among themselves as regards *preparedness* for development. Some are fresh, others old; some are dry, others moist. Infected by such germs the same infusion would require different lengths of time to develop Bacterial life. And this remark, I doubt not, applies to the different degrees of rapidity with which epidemic disease affects different people. In some the hatching-period, if I may call it such, is long, in some short, the differences depending upon the different degrees of preparedness of the contagium *.

§ 25. *Diffusion of Germs in the Air.*

During the earlier observations recorded in this paper, and others not here mentioned, about 100 exposed tubes or flasks had been distributed irregularly in the rooms where the inquiry is conducted. They expanded to nearly 1000 in the end: not one of them escaped infection. A few days always sufficed to cloud the exposed infusions, and fill them with Bacterial life. I placed tubes at various points in the Royal Institution—on the roof of the house outside, in my bed-room, in an upper kitchen, in my study, in the upper and lower libraries, in the theatre, model-room, reading-room, manager's room, and in a kitchen at the bottom of the house below the level of Albemarle Street. All were smitten with putrefaction, and with its invariable associate, *Bacteria*. In the rooms without fires the action was slower than in the warmer rooms; but all the infusions gave way in the end.

Considering the assertions which had been made regarding the scantiness of *Bacteria*-

* The medical student of the future will probably connect these remarks with the following statement of Dr. Murchison:—"In that protean disease typhoid fever, I have repeatedly had occasion to observe a remarkable similarity in the course, and even in the complications, according to the source of the poison."—Trans. Path. Soc. vol. xxvi. p. 315.

germs in the air, observations outside of London would, I thought, be interesting. Accordingly, on the 27th of October, a tube containing an infusion of beef was placed in the hands of Mr. Darwin, who had the kindness to set it in his study at Down and observe its changes. In three days it became cloudy and peopled with *Bacteria*. The same result was obtained in the open air. Mr. Francis Darwin was good enough to expose an infusion for me in his father's orchard: the weather was cold, and the progress, therefore, slow; but the tube which had been exposed on the 2nd of November was cloudy and full of *Bacteria* on the 9th. In Sir John Lubbock's study a similar result was obtained. From Sherwood, near Tunbridge Wells, infusions of fowl and wild duck were returned to me by Mr. Siemens thickly turbid and crowded with *Bacteria*. From Pembroke Lodge, Richmond Park, Mr. Rollo Russell returned tubes of turnip, beef, and mutton swarming with life. An infusion of beef exposed at Heathfield Park, Sussex, for a week was returned to me by Miss Hamilton muddy and filled with *Bacteria*. From Greenwich Hospital Mr. Hirst sent me tubes of beef-, mutton-, and turnip-infusion filled with vigorous *Bacteria*. Dr. Hooker was good enough to take charge of three sets of tubes at Kew. One set was placed in the conservatory, with a temperature of 45° to 50°; one in his own study, with a temperature of 54° to 60°; a third set was placed in the orchid-house (the hottest in the gardens), with a temperature of 62° to 75°.

The tubes were opened on the 4th of December, all of them being then clear. In the orchid-house the turnip became cloudy on the 7th, the two others on the 8th, after which the opacity rapidly increased. In the study all remained clear until the 9th, when the turnip began to cloud. On the 11th the beef was still clear, while the mutton had given way. On the 13th all of them had yielded. In the conservatory the turnip began to cloud on the 10th; the others followed much in the same order as in the other cases.

The influence of temperature seems well shown by these observations. Three days sufficed to cloud the turnip in the orchid-house, five days in the study, and six days in the conservatory. The mutton in the study gathered over it a thick blanket of *Penicillium*. On the 13th it had assumed a light brown colour, "as if by a faint admixture of clay;" but the infusion became transparent. The "clay" here was the slime of dormant or dead *Bacteria*, the cause of their quiescence being the blanket of *Penicillium*. I found no active life in this tube, while all the others swarmed with *Bacteria*. From the Crystal Palace at Sydenham Mr. Price sent me tubes of mutton, beef, and turnip charged with *Bacteria*. The temperature was low at night, the development of life being thereby considerably retarded.

Thus everywhere it has been tested the atmosphere has been found charged with the germs of *Bacteria*.

I wished, however, to obtain clearer and more definite insight as to the diffusion of atmospheric germs. Supposing a large tray to be filled with a suitable organic infusion and exposed to the air. Into it the germs would drop; and could the resulting organisms be confined to the locality where the germs fell, we should have the floating life of the

atmosphere mapped, so to speak, in the infusion. But in such a tray the organisms would intermingle and thus mar the revelation of their distribution. Valuable information I thought might be gained by breaking up the infusion into isolated conterminous patches, and exposing them to the air.

A square wooden tray was accordingly pierced with one hundred circular apertures; into each of which was dropped a test-tube 3 inches long and 1 inch wide, with its rim resting in each case upon the rim of the aperture. There were ten rows of tubes, with ten tubes in each row. On the 23rd of October, 1875, thirty of these tubes were filled with an infusion of hay, thirty-five with an infusion of turnip, and thirty-five with an infusion of beef. The tubes with their infusions had been previously boiled ten at a time in an oil-bath.

One hundred circles were marked upon paper so as to form a plan of the tray, and every day the state of each tube was registered upon the corresponding circle. Seven such maps or records were executed.

I will use the term "cloudy" to denote the early stage of turbidity, distinct but not strong. The term "muddy" will be used to denote thick turbidity.

§ 26. *Tray of one hundred tubes.*

On the 25th of October one or two of the tubes exposed on the 23rd showed signs of yielding; but the progress of putrefaction was first registered on the 26th. Map I., embracing the first record, is annexed (p. 64); it may be thus described.

Hay.—Of the thirty specimens exposed, one had become 'muddy'—the seventh in the middle row reckoning from the side of the tray nearest a stove. Six tubes remained perfectly clear between this muddy one and the stove, proving that differences of warmth may be overridden by other causes. Every one of the other tubes containing the hay-infusion showed spots of mould upon the clear liquid.

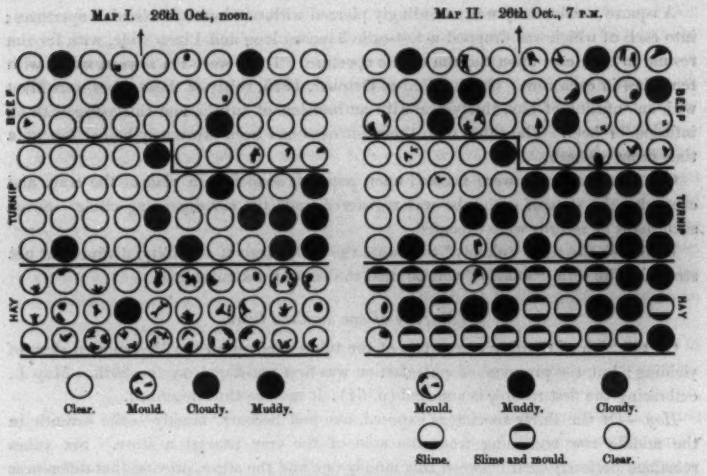
Turnip.—Four of the thirty-five tubes were very muddy, two of them being in the row next the stove, one four rows distant, and the remaining one nine rows away. Besides these, seven tubes had become clouded. There was no mould on any of the tubes.

Beef.—One tube of the thirty-five was quite muddy, in the seventh row from the stove. There were three cloudy tubes, while seven of them bore spots of mould.

As a general rule organic infusions exposed to the air during the autumn remained for two days or more perfectly clear. Doubtless from the first germs fell into them, but they required time to be hatched. This period of clearness may be called the "period of latency;" and, indeed, it exactly corresponds with what is understood by this term in medicine. Towards the end of the period of latency the fall into a state of disease, if I may use the term, is comparatively sudden; the infusion passing from perfect clearness to cloudiness more or less dense in a few hours.

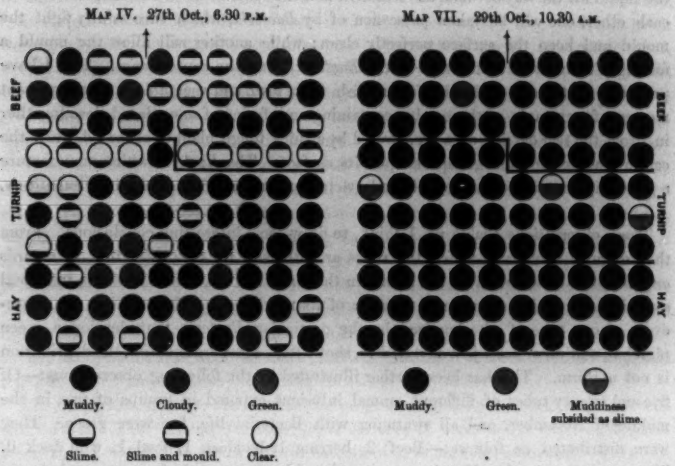
Thus the tube placed in Mr. DARWIN'S possession was clear at 8.33 A.M. on the 19th of October, and cloudy at 4.30 P.M. Seven hours, moreover, after the first record of our tray of tubes, a marked change had occurred. For the purpose of comparison the

second record (Map II.) is placed beside the first. The change may be thus described:—Instead of one, eight of the tubes containing hay-infusion had fallen into uniform muddiness. Nineteen of these had produced Bacterial slime, which had fallen to the bottom,



every tube containing the slime being covered by mould. Three tubes only remained clear, but with mould upon their surfaces. The muddy turnip-tubes had increased from four to ten; seven tubes were clouded, while eighteen of them remained clear, with here and there a speck of mould on the surface. Of the beef, six were cloudy and one thickly muddy, while spots of mould had formed on the majority of the remaining tubes. Fifteen hours subsequent to this observation, viz. on the morning of the 27th of October, all the tubes containing hay-infusion were smitten, though in different degrees, some of them being much more turbid than others. Of the turnip-tubes, three only remained unsmitten, and two of these had mould upon their surfaces. Only one of the thirty-five beef-infusions remained intact. A change of occupancy, moreover, had occurred in the tube which first gave way. Its muddiness remained grey for a day and a half, then it changed to bright yellow-green, and it maintained this colour to the end. On the evening of the 27th every tube of the hundred was smitten, the majority with uniform turbidity, some, however, with mould above and slime below, the intermediate liquid being clear. The whole process bore a striking resemblance to the propagation of a plague among a population, the attacks being successive and of different degrees of virulence. I annex copies of the fourth and seventh maps with their respective dates.

On the 31st of October I finally inspected the tray of tubes. All those containing the hay-infusion were turbid, some thicker and much more deeply coloured than others. They were all at first alike in colour. Out of the thirty tubes four only were free from



mould. Three of these were adjacent to each other, the fourth at a distant portion of the tray.

The *Penicillium* was exquisitely beautiful. Its prevalent form was a circular patch made up of alternate zones of light and deep green. In some cases the liquid was covered by a single large patch; in others there were three or four patches, each made up of its differently coloured zones. Reticulated patterns also occurred. Three kinds of *Penicillium* seemed struggling for existence, namely:—that just described; a second kind, of the same consistency and colour, but forming little rounded heaps instead of circles; thirdly, a woolly, voluminous, white mould, in the middle of which a zoned circle of the other mould sometimes formed a little islet.

All the tubes containing the turnip-infusion were also turbid on the 31st. Nine of them were free from mould. This, where it occurred, exactly resembled small cocoons in shape. The beef-tubes were also all turbid on the 31st, and seventeen of them were free from mould. The mould upon the beef, moreover, was much less luxuriant than that on the hay- and turnip-infusions. The mould-developing power is obviously greatest in the hay-, less in the turnip-, and least of all in the beef-infusion. In every case where the mould was thick and coherent the *Bacteria* died, or became dormant, and fell to the

bottom as a sediment. The growth of mould and its effect on the *Bacteria* are very capricious. The turnip-infusion, after developing in the first instance its myriadfold Bacterial life, frequently rapidly contracts mould, which stifles the *Bacteria* and clears the liquid all the way between the sediment and the scum. Of two tubes placed beside each other, one will be taken possession of by *Bacteria*, which successfully fight the mould and keep the surface perfectly clean; while another will allow the mould a footing, the apparent destruction of the *Bacteria* being the consequence. This I have proved to be the case with all infusions, fish, flesh, fowl, and vegetable. At the present moment, for example, of three tubes containing an infusion of sole, placed close together in a row, the two outside ones are covered by a thick tough blanket of mould, while the central one has not a single speck upon its surface. The *Bacteria* which manufacture a green pigment appear to be uniformly victorious in their fight with the *Penicillium*.

These observations enable us, I think, to draw some interesting conclusions. From the irregular manner in which the tubes are attacked we may infer that, as regards *quantity*, the distribution of the germs in the air is not uniform. A single tube will sometimes be a day or more in advance of its neighbours. The singling out, moreover, of one tube of the hundred by the particular *Bacteria* that develop a green pigment, and other cases just adverted to, shows that, as regards *quality*, the distribution is not uniform. This has been further illustrated by the following observations:—Of five and twenty tubes of different animal infusions exposed in groups of five, in the middle of November, and all swarming with Bacterial life, five were green. They were distributed as follows:—Beef 2, herring 1, haddock 1, fowl 1, wild duck 0. The same absence of uniformity was manifested in the struggle for existence between the *Bacteria* and the *Penicillium*. In some tubes the former were triumphant; in other tubes of the same infusion the latter was triumphant. It would also seem that a want of uniformity as regards *vital vigour* prevailed. With the selfsame infusion the motions of the *Bacteria* in some tubes were exceedingly languid; while in other tubes the motions resembled a rain of projectiles, being so rapid and violent as to be followed with difficulty by the eye. Reflecting on the whole of this, I conclude that the germs float through the atmosphere in groups or clouds, and that now and then a cloud specifically different from the prevalent ones is wafted through the air. The touching of a nutritive fluid by a Bacterial cloud would naturally have a different effect from the touching of it by the interspace between two clouds. But, as in the case of a mottled sky, the various portions of the landscape are successively visited by shade, so, in the long run, are the various tubes of our tray touched by the Bacterial clouds, the final fertilization or infection of them all being the consequence*.

* In hospital practice the opening of a wound during the passage of a Bacterial cloud would have an effect very different from the opening of it in the interspace between two clouds. Certain caprices in the behaviour of dressed wounds may possibly be accounted for in this way.

Under the heading "Nothing New under the Sun," Prof. HUXLEY has lately sent me the following remarkable

The tray of tubes proved so helpful in enabling me to realize mentally the distribution of germs in the air, that on the 9th of November I exposed a second tray containing one hundred tubes filled with an infusion of mutton. On the morning of the 11th six of the ten nearest the stove had given way to putrefaction. Three of the row most distant from the stove had yielded, while here and there over the tray particular tubes were singled out and smitten by the infection. Of the whole tray of one hundred tubes, twenty-seven were either muddy or cloudy on the 11th. Thus, doubtless, in a contagious atmosphere, are individuals successively struck down. On the 12th all the tubes had given way, but the differences in their contents were extraordinary. All of them contained *Bacteria*, some few, others in swarms. In some tubes they were slow and sickly in their motions, in some apparently dead, while in others they darted about with rampant vigour. These differences are to be referred to differences in the germinal matter, for the same infusion was presented everywhere to the air. Here also I imagine we have a picture of what occurs during an epidemic, the difference in number and energy of the Bacterial swarms resembling the varying intensity of the disease. It becomes obvious from these experiments that of two individuals of the same population exposed to a contagious atmosphere, the one may be severely, the other lightly attacked, though the two individuals may be as identical as regards susceptibility as two samples of one and the same mutton-infusion. What I have already said regarding the "preparedness" of contagium has its application here.

The parallelism of these actions with the progress of infectious disease may be traced still further. The 'Times,' for example, of January 17 contained a letter on typhoid fever, signed "M.D.," in which occurs the following remarkable statement:—"In one part of it [Edinburgh], congregated together and inhabited by the lowest of the population, there are, according to the Corporation return for 1874, no less than 14,319 houses or dwellings—many under one roof, on the 'flat' system—in which there are no house connexions whatever with the street-sewers, and, consequently, no water-closets. To this day, therefore, all the excrementitious and other refuse of the inhabitants is collected in pails or pans, and remains in their midst, generally in a partitioned-off corner of the living-room, until the next day, when it is taken down to the streets and emptied into the Corporation carts. Drunken and vicious though the population be, herded together like sheep, and with the filth collected and kept for 24 hours in their very midst, it is a remarkable fact that typhoid fever and diphtheria are simply unknown in these wretched hovels."

The analogy of this result with the behaviour of our infusions is perfect. On the 30th of November, for example, a quantity of animal refuse, embracing beef, fish, rabbit, hare, was placed in two large test-tubes opening into a protecting-chamber con-

extract:—'Uebrigens kann man sich die in der Atmosphäre schwimmenden Thierchen wie Wolken denken, mit denen ganz leere Luftmassen, ja ganze Tage völlig reinen Luftverhältnisse wechseln.' (Ehrenberg, 'Infusionsthierchen,' 1838, p. 525.) The coincidence of phraseology is surprising, for I knew nothing of Ehrenberg's conception. My 'clouds,' however, are but small miniatures of his.

taining six tubes. On December 13, when the refuse was in a state of noisome putrefaction, infusions of whiting, turnip, beef, and mutton were placed in the other four tubes. They were boiled and abandoned to the action of the foul "sewer-gas" emitted by their two putrid companions. On Christmas-day these four infusions were limpid. The end of the pipette was then dipped into one of the putrid tubes, and a quantity of matter, comparable in smallness to the pock-lymph held on the point of a lancet, was transferred to the turnip. Its clearness was not sensibly affected at the time; but on the 26th it was turbid throughout. On the 27th a speck from the infected turnip was transferred to the whiting; on the 28th disease had taken entire possession of the whiting. To the present hour the beef- and mutton-tubes remain as limpid as distilled water. Just as in the case of the living men and women in Edinburgh, no amount of fetid gas had the power of propagating the plague, as long as the organisms which constitute the true contagium did not gain access to the infusions.

In the foregoing observations the tubes were arranged in the same horizontal plane; but I also sought to obtain some notion of the vertical distribution of the germs in the air of the room. Two trays, each containing 100 tubes, were supported the one above the other in the same frame. The upper tray had all the air between it and the ceiling, a height of about 12 feet, from which the germs might descend upon it; the lower tray was shaded by the upper, a space of only 6 inches existing between them. If the number of germs deposited in the tubes were determined by the air-space above, the upper tray would be the one most rapidly and thoroughly taken possession of. The reverse was the case. As regards the development of Bacterial life, the lower tray was from first to last in advance of its neighbour. It is not air-space, then, so much as stillness, that determines the deposition of the germs. The air between the two trays being less disturbed than the general air of the room, the germs were less wafted about, and therefore fell in greater numbers into the tubes of the lower tray. We have here data which will enable us to form a rough notion of the lower limit of the number of germs contained in the room where the experiments were made.

The floor of the room measured 20 feet by 15 feet; its area was therefore 43,200 square inches, and every square inch would afford room for the section of one of our test-tubes. The height of the room is 180 inches; hence 30 layers of tubes 6 inches apart might be placed one above the other between the floor and ceiling. This would make 1,296,000 tubes. If only a single germ a day fell into each tube this would be the number of the germs. If the number deposited were one an hour, we should have thirty millions a day sown in the tubes. Probably the average time necessary for infection is very much less than an hour. At all events 30,000,000 of germs daily would be an exceedingly moderate estimate of the number falling into our thirty layers of tubes. This, moreover, would only be a fraction—probably a small fraction—of the germs really present in the air. In his Presidential Address to the British Association at Liverpool, Prof. HUXLEY ventured the statement that myriads of germs are floating in our atmosphere. Untrained experimenters and rash reasoners have ridiculed this state-

ment. In view of the foregoing calculation it, however, expresses the soberest fact Indeed, taking the word myriad in its literal sense of ten thousand, it would be simple bathos to apply it to the multitudinous germs of our air.

§ 27. *Some Experiments of* PASTEUR *and their Relation to Bacterial Clouds.*

Quite recently I had occasion to refresh my memory of PASTEUR's paper published in the 'Annales de Chimie' for 1862. The pleasure I experienced on first reading it was revived by its reperusal. Clearness, strength, and caution, with consummate experimental skill for their minister, were rarely more strikingly displayed than in this imperishable essay. Hence it is that during recent discussions, in which this and other labours of the highest rank met with such scant respect, those in England most competent to judge of the value of scientific work never lost faith in the substantial accuracy of PASTEUR. One striking example of his penetration has an immediate bearing on the conclusion regarding Bacterial clouds, independently drawn by me from the deportment of the tray of one hundred tubes. On the 28th of May, 1860, PASTEUR opened, on an uncovered terrace a few metres above the ground, four flasks containing the water of yeast. Nothing appeared in any of them until the 5th of June, when a small tuft of mycelium was observed in one of them. On the 6th a second tuft appeared in another flask; the two remaining flasks remained intact and without organisms. On the 20th of July he opened, in his own laboratory, six flasks containing water of yeast. Four of them remained perfectly intact, while two of them became promptly charged with organisms. PASTEUR infers from these observations the non-continuity of the cause to which so-called spontaneous generation is due. This inference is quite in accord with the notion of Bacterial clouds suggested by my observations. PASTEUR, in fact, sometimes opened his flask in the midst of a Bacterial cloud and obtained life, sometimes in the interspace between two clouds, and obtained no life.

Not with a view of repeating this observation, which had been forgotten, but for another reason, I opened on the 6th of January last a number of hermetically sealed tubes in one and the same room of the Royal Institution. The names of the infusions contained in the tubes, the date of sealing them up, their condition before opening on the 6th, and their appearance six days subsequently on the 12th are given in the accompanying statement. I chose for these observations tubes which contained a little liquid in their drawn-out portions. In every case the motion of this liquid, when the tube was broken, indicated a violent inrush of air.

Infusion.	Date of sealing.	Appearance, Jan. 6.	Appearance, Jan. 12.
Grouse	Nov. 27th	Clear . .	Clear.
Sole	,, 17th	,, . .	Turbid.
Turnip No. 1	Oct. 5th	,, . .	Penicillium on surface.
Turnip No. 2	,, ,,	,, . .	Clear.
Hay	,, ,,	,, . .	Mycelium at bottom.
Wild Duck	Nov. 12th	,, . .	Turbid.

Infusion.	Date of sealing.	Appearance, Jan. 6.	Appearance, Jan. 12.
Mutton	Nov. 12th	Clear	Cloudy.
Fowl	„ „	„	Clear.
Beef	„ „	„	Mycelium at bottom.
Haddock	„ „	„	Clear.
Sweetbread	„ 16th	„	Mycelium at bottom.
Rabbit	„ 13th	„	Clear.
Heart	„ „	„	Curdy layer at top.
Pheasant	„ „	„	Clear.
Mullet	„ „	„	„
Hare	„ „	„	„
Snipe	„ „	„	„
Partridge	„ „	„	„
Plover	„ „	„	Mycelium below.
Codfish	„ „	„	Clear.
Kidney	Jan. 5th	„	Mycelium at bottom.
Salmon	Dec. 13th	„	Clear.
Whiting	„ „	„	„
Turnip	„ 29th	„	„
Hay 4 drops of caustic potash	Nov. 22nd	Clear with sediment	Mycelium at bottom.
Hay 2 drops of caustic potash	„ „	Clear	Mycelium at bottom.
Hay 5 drops of caustic potash	„ „	Clear with sediment	Clear.
Hay 6 drops of caustic potash	„ „	Clear with sediment	„
Liver	Nov. 30th	Clear.	
Hay	„ 18th	„	Clear.
Hay	„ „	„	„
Turnip	„ „	„	Muddy.

Thus, out of 31 flasks opened in the same air, 18 remained intact, while 13 were taken possession of by organisms—a fact obviously the same in character as that described by PASTEUR. Such experiments demonstrate, if demonstration were needed, that it is not the air itself, or any gaseous or vaporous substance uniformly diffused through it, but some discontinuous substance floating in it, that is the cause of the infection. Instead of our tubes let us suppose thirty-one wounds to be opened in the same ward of a hospital; plainly what has occurred with the tubes may occur with these wounds—some may receive the germs and putrefy, others may escape. Helped by the conception not only of germs, but of germ-clouds, the different behaviour of wounds

subjected apparently to precisely the same conditions will cease to be an inscrutable mystery to the surgeon*.

During the course of this inquiry some eminent biologists have been good enough, from time to time, to look in upon my work, and to give me their views regarding the evidential force of the experiments. To Professor HUXLEY, moreover, I am indebted for undertaking the examination of a number of the hermetically sealed tubes. Thirty of them were placed in his hands, none of them being regarded as defective. A close examination, however, disclosed in one of them a mycelium. No faultiness could for a time be discovered in the tube; the sealing appeared to be quite as perfect as that of its sterile fellows. Once, however, on shaking it a minute drop of liquid struck my friend's face; and he soon discovered that an orifice of microscopic minuteness had been left open in the nozzle of the tube. Through this the common air had been sucked in as the liquid cooled, and hence the contamination. It was the only defective tube of the group of thirty, and it alone showed signs of life.

The statement of this fact before the Royal Society, by Prof. HUXLEY, brought to my mind a somewhat similar experience of my own. One morning in November I lifted one of the hermetically sealed tubes from the wire on which it was suspended, and, holding it up against the light, discovered, to my astonishment, a beautiful mycelium flourishing at the bottom. Before restoring the tube to its place I touched its fused end and found it sharp. Close inspection showed that the nozzle had been broken off; the common air had entered, and the seed of the mycelium had been sown. Two other instances, one like that observed by Prof. HUXLEY, have since come to light. In one of them a minute orifice remained after the supposed sealing of the tube. The other case was noticed when the tubes were returned from the Turkish Bath. One of them contained a luxuriant mycelium. It was noticed that the liquid in this tube had singularly diminished in quantity, and on turning the tube up it was found cracked at the bottom.

No case of pseudo-spontaneous generation ever occurred under my hands that was not to be accounted for in an equally satisfactory manner.

In this inquiry, thus far, I have confined my observations to purely liquid infusions, purposely excluding milk, mixtures of turnip-juice and cheese, and, indeed, mixtures of

* "We have ample facts of experiment in our hands," said Mr. KNOWSLEY THORNTON (Trans. of the Pathological Society, vol. xxvi. p. 313), "to show that it is not the gases of the air, or any soluble material in water, but something 'particulate' which sets up all the train of changes in an open wound, which may, after the patient has passed through a period of more or less constitutional disturbance, end in the healing of the wound, or may end in septicæmia and death. This particulate material, then, I believe we have evidence enough to prove consists of germs of *Bacteria* and other low organisms." All the evidence points to this conclusion. I may say that I entirely agree with Mr. THORNTON in the distinction he draws between *germs* and developed *Bacteria* floating in the air. It is, in my opinion, of the very last importance to seize this distinction with clearness. When it is fully realized we shall probably hear less of the arguments against Bacterial contagia founded on the fact that a virus diminishes in strength as the *Bacteria* multiply. A portion of the energy of the virus consists in its passage from the germ state to that of the finished organism.

solids and liquids of all kinds. The next section of the investigation will be devoted to these and kindred subjects; and to it I also postpone the complete examination of *pepton*, and of the remarkable experiments described by Dr. WILLIAM ROBERTS, a small residue of which only I have failed to corroborate.

Throughout the whole of this investigation I have had to congratulate myself on the zealous and efficient aid of my excellent assistant, Mr. JOHN COTTRELL. His intelligence in seizing my ideas, and his mechanical skill in realizing them, have rendered me admirable service. Without such aid, indeed, so much ground could not have been covered in the time. Mr. COTTRELL's junior colleague, Mr. FRANK VALTER, has also acquitted himself to my entire satisfaction.

Royal Institution, 5th April, 1876.

It gives me special pleasure to direct attention here to a paper by the Rev. W. H. DALLINGER, for an advanced proof of which I am indebted to the courtesy of Dr. LAWSON, editor of the 'Popular Science Review.' Mr. DALLINGER and his colleague Dr. DRYSDALE are known to have pushed the microscope to its utmost power of performance at the present time. Their 'Researches into the Life-History of the Monads' are models of scientific thoroughness and concentration. Mr. DALLINGER's review of the present position of the doctrine of spontaneous generation, his remarks on Bacterial germs in relation to the limits of the powers of the microscope, his demonstration that the germs of monads survive in a medium raised to a temperature which destroys the adult, and that precipitated mastic particles like those mentioned in § 16 of this paper are not to be discerned by a magnifying-power of 15,000 diameters, constitute a most interesting and important communication.

NOTE I. *Action of* Bacteria *upon a Beam of Light.*

To trace the gradual growth and multiplication of the *Bacteria* by their action on a beam of light an infusion of beef was prepared on the 5th of October, placed in a globular flask of about 50 cubic inches capacity, and put aside with its mouth open to the laboratory air. On the 8th, 9th, 10th, 11th, and 12th similar flasks were prepared and put aside in succession. On the 12th all the flasks were examined by the concentrated electric light. The freshest one showed the track of the beam as a richly coloured green cone. The green light was unaffected by a NICOL's prism, which, however, quenched the ordinary scattered light and augmented the purity and vividness of the green. It was a case of fluorescence. In the second flask, one day old, the fluorescent beam was in great part masked by the scattered light; the latter, however, could be partially quenched by a NICOL's prism, the purity of the fluorescence being thus in part restored. Through the third flask, two days, and the fourth flask, three days old, the track of the beam was still discernible; through the fifth flask, four days old, it was all

but obliterated, while in the sixth flask, seven days old, it was entirely shattered, the turbid medium being filled uniformly with the laterally scattered light.

Two of these flasks were of a bright yellow-green colour, two were milky or white, and two of a dull brownish hue.

Cohn mentions the bluish tinge of the infusion by reflected and its yellow tinge by transmitted light when the *Bacteria* are incipient. This is due to a dichroitic action, similar to that which produces the blue of the sky and the morning and evening red. The blue, however, though discernible, is not pronounced, for the *Bacteria* are too large to scatter the colour in any high degree of purity; but with a "muddy" infusion a very fair red may be obtained from transmitted light. I have used the Bacterial turbidity for photometric purposes. On the 9th of October, for example, I accompanied Sir Richard Collinson and a Committee of the Elder Brethren of the Trinity House to Charlton, with the view of comparing together two lights mounted at the Trinity Wharf at Blackwall. To imitate a foggy atmosphere, I employed an infusion cloudy with *Bacteria* and placed in a glass cell. With it the beams could be toned gradually down to complete extinction.

Note II. *Fluorescence of Infusions.*

All the animal infusions, both flesh and fish, showed the same fluorescence. It was the same green hue throughout, though of varying degrees of intensity. In wild duck, grouse, snipe, hare, partridge, and pheasant the fluorescence was fine—sometimes exceedingly fine. In rabbit it was less fine than in hare, and in a tame rabbit less fine than in a warren rabbit. Fishes also differed from each other. Mullet, for example, was finer than cod, herring, or haddock. Beef, mutton, heart, liver all showed the same green fluorescence.

Led up to it by a series of remarkable experiments on the rapidity of the passage of crystallized substances into the vascular and non-vascular textures of the body*, Dr. Bence Jones and Dr. Dupré communicated to the Royal Society in 1867 a highly interesting paper "On a Fluorescent Substance, resembling Quinine, in Animals"†. They then showed that "from every texture of man and of some animals a fluorescent substance can be extracted, which, when extracted, has a very close optical and chemical resemblance to quinine." They therefore called it animal quinoidine. In dilute solutions they found that the fluorescence of the animal substance was not to be distinguished from that produced by quinine. When the solution was concentrated, the colour of the light was of a decidedly greenish hue. This latter observation is most in agreement with mine. In all the infusions examined by me the fluorescent light was a decided green, and not to be mistaken for the blue light of quinine.

The green colour is similar to that emitted by the crystalline lens when a beam of

* Proceedings of the Royal Society, vol. xiv. 1865.

† Ibid. vol. xv. p. 73.

violet light impinges on it *; sending such a beam through any of the infusions, the "degradation" of the violet to green is strikingly illustrated.

The foregoing statement refers to the deportment of the infusions after boiling and filtering. Prior to boiling some of them were of a brilliant ruby colour; but even here, when the layer of liquid between the eye and the beam was not too thick, the green fluorescence could be seen through the red liquid.

* On plunging the eye into the beam of the electric lamp, transmitted through violet glass, the moment the crystalline lens is seen to fluoresce by a second observer, a blue shimmer is seen by the eye on which the beam falls. In the case of my own eye, I can always readily tell when the fluorescence has set in.

III. *The Absolute Direction and Intensity of the Earth's Magnetic Force at Bombay, and its Secular and Annual Variations.* *By* CHARLES CHAMBERS, *F.R.S., Superintendent of the Colaba Observatory.*

Received October 26, 1871,—Read January 25, 1872*.

THE observations discussed in this paper were taken at the Colaba Observatory during the years 1867 to 1874, and consist of observations of Dip, Declination, and Horizontal Intensity. The instruments with which they were taken were a Dip-circle by BARROW, with 3½-inch needles, and a Unifilar Magnetometer by ELLIOTT BROTHERS, and both were examined and approved at the Kew Observatory before being sent out to India in the year 1867. Complete observations were taken regularly of the Dip and Horizontal Force twice a week, and of the Declination once a week.

Data for Investigation.—These consist of the monthly means of the determinations of Absolute Dip from April 1867 to March 1874, and the monthly means of the determinations of Absolute Declination and Absolute Horizontal Intensity from July 1867 to December 1873.

I. *Dip.*

2. For some unexplained reason, but which is suspected to be owing to a sudden deterioration in the axles of the dip-needles, the quality of the observations began in March 1870 to be of a decidedly inferior order to that of the earlier observations; and the efforts made to obtain new needles, of the high-class character of those first supplied with the dip-instrument, have hitherto been unsuccessful, possibly because some secret process in their production has died with the maker. For this reason the first three years' observations will alone be treated in some detail, and the monthly and annual means of the last four years will be simply recorded.

Monthly Mean Values.—The following Table shows the monthly mean values of the Dip from April 1867 to March 1870:—

TABLE I.

Year.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
	19° +	19° +	19° +	19° +	19° +	19° +	19° +	19° +	19° +	19° +	19° +	19° +
1867–68	1'·1	1'·9	1'·5	0'·8	2'·2	2'·5	2'·5	2'·8	2'·7	2'·7	3'·4	3'·8
1868–69	4·1	4·1	4·3	4·3	4·2	4·3	4·2	3·6	3·5	3·7	4·8	5·2
1869–70	6·0	6·2	6·3	6·8	6·4	5·7	6·2	6·5	5·6	5·6	5·8	6·0

* I have taken the opportunity, which the lapse of time affords, of extending the number of years of observations treated in the paper from 3½ to 6½.—*July*, 1876.

3. *Annual Mean Values and Secular Change.*—The annual mean values and yearly increments are as follows:—

TABLE II.

Year.	Mean Dip.	Annual Increase of Dip.
1867–68	19° 2′·3	
1868–69	19 4·2	+1′·9
1869–70	19 6·1	+1·9
Mean Dip for three years...	19 4·2	

The two yearly differences agree in making the annual secular change of dip a steady increase of 1′·9; hence the mean dip for the three years, 19° 4′·2, will properly correspond to the mean epoch, which is the 1st October, 1868.

4. *Annual Variation.*—The average monthly values of dip for the period of three years, shown below, are affected by secular change; this is eliminated, on the assumption that the change is uniform from month to month, by subtracting from the values for the months May to March respectively once, twice, thrice, &c. the monthly secular increase (0′·16).

TABLE III.

Month	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Mean Monthly Dip for period of three years... } 19°+	3′·7	4′·1	4′·0	4′·0	4′·3	4′·2	4′·3	4′·3	3′·9	4′·0	4′·7	5′·0
Correction for secular change, to April 15, 1868 }	0	−0·2	−0·3	−0·5	−0·6	−0·8	−1·0	−1·1	−1·3	−1·4	−1·6	−1·8
Monthly values cleared of } 19°+ secular change.....	3·7	3·9	3·7	3·5	3·7	3·4	3·3	3·2	2·6	2·6	3·1	3·2

The means of different groups of the monthly values thus cleared of secular change, but affected by the annual variation of dip, are:—

For April to September	19° 3′·6	Corrected for secular change to epoch April 15, 1868.
„ October to March	19 3·0	
„ May to August	19 3·7	
„ March, April, September, and October .	19 3·4	
„ November to February	19 2·9	

which all agree in indicating an annual variation, in which the dip is a maximum when the sun is about its most northerly position in declination, a minimum when the sun is about its most southerly position, and having intermediate values when the sun is near the equator. The semiannual excess of dip when the sun has north declination above the mean value for the year is 0′·3.

5. *Diurnal Inequality at Observation-hours.*—The difference between the morning and afternoon observations is almost inappreciable, as will be seen by the following statement, which embraces every observation in 1867 and 1868, finished before 15 hours or commenced after 15 hours, for every month in which observations of both kinds are recorded; the general result is a slight excess of dip in the afternoon:—

TABLE IV.

Period.	Needle No.	Number of Observations.	Mean Time of Observation.				Mean Dip.	Excess of Afternoon over Morning.
			First half.		Last half.			
			Commencement.	Conclusion.	Commencement.	Conclusion.		
			h m	h m	h m	h m	° ′	
1867, June to December	1	17	10 22	10 56	11 4	11 47	19 1·0	+0·3
" " "	1	13	15 20	15 50	16 5	16 38	19 1·3	
" " "	2	15	10 23	10 58	11 19	11 50	19 3·3	0·0
" " "	2	15	15 26	15 55	16 11	16 41	19 3·3	
1868, January to December ...	1	26	10 25	10 49	10 59	11 25	19 3·2	+0·1
" " " ...	1	26	15 24	15 51	16 0	16 25	19 3·3	
" " " ...	2	27	10 18	10 44	10 54	11 21	19 4·4	+0·1
" " " ...	2	25	15 24	15 49	15 59	16 24	19 4·5	

From this it may be inferred that the annual variation of the diurnal inequality of dip for the mean observation hour (or rather the mean variation for the morning and afternoon hours) is also probably small, and may scarcely affect sensibly the annual variation of dip found above; this latter variation must, however, be accepted subject to correction, if necessary, when the annual variation of the diurnal inequality of dip has been well determined.

6. *Probable Error.*—It will suffice to give an idea of the quality of the observations of dip if an account be here given of the results of determinations, made early in 1869, of the probable error of a single weekly determination (being the mean of a pair of observations) in three distinct periods in 1867 and 1868. The semiannual inequality found, by a similar process to that described above, from this more limited body of observations was the same as that found above from three years' observations, viz. an excess of 0′·3 in the dip from April to September above the mean of the year, and an equal defect during the opposite half-year. The annual secular increase of dip was found to be 1′·3. These values were embodied in formulæ for correcting the observed weekly values of dip to a common epoch as follows:—

From April 29 to August 16, 1867,

$$\theta = \theta' - 0'{\cdot}1\, m,$$

m being the excess (in months) of the date over June 15, 1867;

From August 23 to September 27, 1867,

$$\theta = \theta' - 0'{\cdot}1\, m - 0'{\cdot}3;$$

From October 1 to December 31, 1867,

$$\theta = \theta' - 0'{\cdot}1\, m + 0'{\cdot}3,$$

m being the excess of the date (in months) over October 15, 1867;

From January 1 to March 31, and from October 1 to December 31, 1868,

$\theta = \theta' - 0'{\cdot}1\ m + 0'{\cdot}3$,

And from April 1 to Sept. 30, 1868,

$\theta = \theta' - 0'{\cdot}1\ m - 0'{\cdot}3$,

m being the excess of the date (in months) over July 15, 1868,—

θ in every case representing the dip at the common epoch of the period, and θ' the observed dip.

The weekly values of dip being thus corrected, the differences were taken between them and the mean of all the corrected values in each period, and to these differences the method of least squares was applied to find the probable errors for the several periods; these are:—

For April 29 to August 16, 1867, the probable error $= \pm 0'{\cdot}67$,
„ August 23 to December 31, 1867 „ „ $= \pm 0'{\cdot}26$,
„ January 1 to December 31, 1868 „ „ $= \pm 0'{\cdot}24$.

The remaining observations, of 1869 and 1870, being of about the same quality as those of 1868 will have about the same probable error.

The unusual smallness of the probable error of a weekly determination since August 17, 1867, is attributable mainly, I think, to the comparative infrequency and moderate amount of disturbance at a low latitude station, but partly also to the extreme care that has been given to secure the perfect preservation of the axles of the needles; the needles themselves also appear to be of excellent character.

7. *Differences with different needles.*—The mean dip observed with needle No. 2 has, at different periods, exceeded that observed with needle No. 1, as shown below:—

TABLE V.

Period.	Excess of Dip with Needle No. 2 over that with Needle No. 1.	
	Morning observations.	Afternoon observations.
1867, June to August	$+5'{\cdot}0$	$+5'{\cdot}0$
„ September to December	$+0{\cdot}2$	$-0{\cdot}2$
1868, January to December	$+1{\cdot}2$	$+1{\cdot}2$

It is noticeable that the great change between the two first periods is contemporaneous with the introduction of the practice of remagnetizing the needle before commencing an observation.

8. *Monthly Mean Values of the Dip from April* 1870 *to March* 1874.—

TABLE VI.

Year.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
	°	°	°	°	°	°	°	°	°	°	°	°
	19+	19+	19+	19+	19+	19+	19+	19+	19+	19+	19+	19+
1870–71.....	10·6	12·4	8·0	7·0	2·5	1·3	7·4	6·4	8·8	1·9	12·8	12·7
1871–72.....	14·1	7·0	0·2	5·7	9·3	11·5	9·7	9·2	11·2	11·5	11·9	11·7
1872–73.....	12·8	14·3	14·4	15·0	14·2	14·2	15·3	14·7	15·6	14·4	14·4	16·7
1873–74.....	16·7	16·4	15·6	14·6	12·8	12·9	14·2	13·7	13·7	14·2	14·9	13·8

On and after September 21, 1871, the place of observation was changed from the basement of the Electrometer Tower to the top room of the same building, the former height above the ground having been 6 feet and the present height being 38 feet.

9. *Annual Mean Values of the Dip and Annual Increase of Dip for seven years.*—

TABLE VII.

Year.	Mean Dip.	Annual Increase of Dip.
	° ′	′
1867-68	19 2·3	
1868-69	19 4·2	+1·9
1869-70	19 6·1	+1·9
1870-71	19 7·6	+1·5
1871-72	19 9·5	+1·9
1872-73	19 14·8	+5·3
1873-74	19 14·5	−0·3
Mean Dip for seven years.	19 8·4	Corresponding to epoch October 1, 1870.

II. *Declination.*

10. *Monthly Mean Values.*—In Table VIII. are collected the monthly means of the values of absolute declination, as observed from July 1867 to December 1873, and the corresponding mean readings of the large declination magnetometer; and in Table IX. are shown the same mean values of declination, corrected for the difference between the corresponding mean readings of the large declination magnetometer and the mean readings of that instrument (also given with the same Table) for the respective months, the corrected values thus obtained showing the mean declination of the several months. The adopted value of a unit of the scale of the large declination magnetometer is 6′ 49″·5, increasing readings denoting increasing easterly declination.

TABLE VIII.

Month.	Mean Observed Declination.							Corresponding Mean Scale-reading of large Declination Magnetometer.						
	1867.	1868.	1869.	1870.	1871.	1872.	1873.	1867.	1868.	1869.	1870.	1871.	1872.	1873.
	′ ″	′ ″	′ ″	′ ″	′ ″	′ ″	′ ″							
January.....	.....	44 18	46 15	47 9	49 7	53 11	55 6	.....	35·25	35·55	35·70	36·13	36·59	36·50
February	.....	44 2	46 56	47 4	50 18	52 43	53 2	.....	35·30	35·54	35·73	36·26	36·53	36·50
March	.....	44 56	46 22	48 4	49 32	50 57	52 35	.....	35·22	35·46	35·88	36·13	36·23	36·47
April	.....	43 19	45 7	46 36	48 31	50 45	53 14	.....	35·12	35·28	35·64	35·94	36·20	36·53
May	.....	42 27	45 26	47 0	49 11	50 29	52 00	.....	35·12	35·38	35·67	36·01	36·17	36·30
June	.....	42 24	45 38	46 54	48 37	51 6	52 20	.....	35·07	35·38	35·63	35·92	36·24	36·36
July	41 34	43 24	45 57	47 17	48 48	50 6	52 53	34·86	35·25	35·47	35·66	35·95	36·09	36·41
August	41 15	43 39	45 16	46 43	49 10	51 6	51 15	34·80	35·21	35·58	35·62	35·97	36·21	36·16
September.....	41 20	42 31	45 15	47 23	48 50	50 8	51 49	34·78	35·14	35·46	35·70	35·97	36·05	36·30
October	42 18	44 51	46 29	49 15	50 6	52 46	52 46	34·92	35·47	35·62	36·02	36·10	36·47	36·47
November	43 38	46 4	47 13	49 47	51 31	52 35	52 59	35·08	35·59	35·73	36·17	36·31	36·44	36·51
December	43 58	45 34	47 43	50 7	51 52	52 58	53 36	35·19	35·44	35·74	36·22	36·37	36·48	36·64

TABLE IX.

Month.	Mean Monthly Declination reduced to Mean Monthly Reading of the large Declination Magnetometer.							Mean Monthly Reading of large Declination Magnetometer.						
	1867.	1868.	1869.	1870.	1871.	1872.	1873.	1867.	1868.	1869.	1870.	1871.	1872.	1873.
	′ ″	′ ″	′ ″	′ ″	′ ″	′ ″	′ ″							
January	.....	44 8	45 55	48 27	49 52	52 26	53 51	.....	35·23	35·50	35·89	36·24	36·48	36·61
February	.....	43 54	47 0	48 14	50 26	52 43	53 43	.....	35·28	35·55	35·90	36·28	36·53	36·60
March	.....	44 52	47 15	48 33	50 46	52 52	53 49	.....	35·31	35·59	35·95	36·31	36·51	36·65
April	.....	45 14	47 30	48 55	51 3	52 52	53 55	.....	35·40	35·63	35·98	36·31	36·51	36·63
May	.....	44 26	47 37	48 51	50 53	52 40	53 51	.....	35·41	35·70	35·94	36·26	36·49	36·57
June	.....	44 43	47 49	48 57	50 44	52 48	54 2	.....	35·41	35·70	35·93	36·23	36·49	36·61
July	43 16	44 38	47 23	49 16	51 3	52 38	54 14	35·11	35·43	35·68	35·95	36·28	36·46	36·61
August	43 6	45 38	47 47	49 39	51 37	53 13	54 36	35·07	35·50	35·75	36·05	36·33	36·52	36·65
September	43 35	45 31	47 38	50 35	51 22	53 12	54 12	35·11	35·58	35·81	36·17	36·34	36·51	36·65
October	43 56	46 1	47 47	50 37	52 1	53 43	54 0	35·16	35·64	35·81	36·22	36·38	36·61	36·65
November	44 19	45 56	47 50	50 7	52 28	53 45	53 56	35·18	35·57	35·82	36·22	36·45	36·61	36·65
December	43 58	45 42	48 20	50 8	52 21	53 47	53 48	35·19	35·46	35·83	36·21	36·44	36·60	36·67

11. *Annual Mean Values and Secular Change.*—Table X. shows the Absolute Declination, both as observed and corrected as in Table IX., for each year from 1867 to 1873, and also the respective annual increments of declination and the mean annual increment for the period of six and a half years.

TABLE X.

Year.	Absolute Declination and Annual Increments.			
	As observed.		Corrected to Mean Reading of large Declination Magnetometer.	
	Declination.	Annual Increment.	Declination.	Annual Increment.
	′ ″		′ ″	
1867, July to December	42 20		42 42	
1868, July to December	44 20	[+2′ 0″]	45 34	[+1′ 52″]
1868, January to December	43 57		45 4	
1869, January to December	46 8	+2 11	47 29	+2 25
1870, January to December	47 47	+1 39	49 21	+1 52
1871, January to December	49 38	+1 51	51 13	+1 52
1872, January to December	51 34	+1 56	53 3	+1 50
1873, January to December	52 38	+1 4	54 0	+0 57
Mean for 6½ years	48 8	+1 46	49 32	+1 48

The values 48′ 8″ and 49′ 32″ of absolute easterly declination, as observed and as corrected, correspond to the mean epoch October 1, 1870; the annual increase of declination (1′ 46″ or 1′ 48″) differs by a scarcely appreciable amount, whether it is derived directly from the observations or from the observations corrected. In calculating the means only half weight has been given to the values in brackets, which are derived from only half as many observations as the other values.

12. *Annual Variation.*—The means for the period of six and a half years of easterly declination in each month are shown below, both as observed and corrected; the cor-

rections for secular change to reduce the values for each month to the same epoch (October 1, 1870), being at the rate of 9″ per month, are also shown, as are likewise the mean monthly values cleared of secular change and the monthly excesses above the mean of the year.

TABLE XI.—Monthly Mean Values of Absolute Declination, as observed.

Month.....	Jan.	Feb.	March.	April.	May.	June.	July.	August.	Sept.	Oct.	Nov.	Dec.	Year.
Mean Declination...	48 51	49 1	48 44	47 55	47 45	47 50	47 8	46 53	46 45	48 22	49 7	49 24	
Correction for secular change ...	+ 22	+ 13	+ 4	− 4	− 13	− 22	+ 22	+ 13	+ 4	− 4	− 13	− 22	
Corrected to epoch October 1, 1870	49 13	49 14	48 48	47 51	47 32	47 28	47 30	47 8	46 49	48 18	48 54	49 2	48 9
Annual Variation...	+1 4	+1 5	+0 39	−0 18	−0 37	−0 41	−0 39	−1 1	−1 20	+0 9	+0 45	+0 53	

TABLE XII.—Monthly Mean Values of Absolute Declination, reduced to Mean Monthly Reading of the large Declination Magnetometer.

Month.....	Jan.	Feb.	March.	April.	May.	June.	July.	August.	Sept.	Oct.	Nov.	Dec.	Year.
Mean Declination...	49 8	49 20	49 41	49 53	49 43	49 50	48 55	49 22	49 26	49 44	49 46	49 43	
Correction for secular change ...	+ 22	+ 13	+ 4	− 4	− 13	− 22	+ 22	+ 13	+ 4	− 4	− 13	− 22	
Corrected to epoch October 1, 1870	49 28	49 33	49 45	49 51	49 30	49 28	49 17	49 35	49 30	49 40	49 33	49 21	49 33
Annual Variation...	−0 5	0 0	+0 12	+0 18	−0 3	−0 5	−0 16	+0 2	−0 3	+0 7	0 0	−0 12	

The two sets of monthly differences represent the annual variation of declination, first, as affected by the annual variation of the diurnal inequality at the usual observation hour, and, secondly, after the elimination of that affection; it is seen at a glance that the effect of the diurnal inequality is to alter both the character and range of the apparent annual variation, raising the range from 0′ 34″ to 2′ 25″, and impressing upon the variation high values during the winter and low values during the summer months—effects quite consistent with the known character of the annual variation of diurnal inequality. The true (corrected) annual variation has a systematic character, with a double oscillation in the period, showing maxima near the times of the equinoxes, and minima about the times of the solstices.

13. That the Declination is greater near the equinoxes than near the solstices may also be shown without assuming a value for the annual secular change; for if this change be uniform the means for the months January and December, February and November, &c. . . . . June and July, will all correspond to the same epoch and be directly comparable; these means are as follows:—

January and December	49	24
February and November	49	33
March and October	49	42
April and September	49	40
May and August	49	32
June and July	49	22

the large values occurring in the middle of the column near the time of the equinoxes. The mean for the months April to September is 49′ 31″, and that for the months January to March and October to December 49′ 33″, showing a scarcely appreciable amount of semiannual inequality.

14. *Probable Error.*—The probable error of a single determination of Absolute Declination has been calculated separately for each of the years 1868 to 1870. The numbers of observations made in those years are 53, 53, and 57 respectively, and each one was reduced to the constant reading 35·00 of the large Declination Magnetometer. If there was no error of observation, and if the large Declination Magnetometer was perfect, these reduced values ought all to be alike, and the degree of accordance existing amongst them will indicate the extent to which these conditions are fulfilled. The differences being taken for each year between each individual reduced value of the Declination and the means of all the values for that year, the probable error of a single determination was found from these differences by the usual method (of least squares) to be ±22″·5, ±22″·0, and ±15″·4 for the years 1868, 1869, and 1870 respectively; and the probable error of the annual means to be ±3″·1, ±3″·0, and ±2″·0 respectively.

III. *Horizontal Force.*

15. *Monthly Mean Values.*—In Table XIII. are collected the mean monthly values, as observed, of the Horizontal Force for the period from July 1867 to December 1873, and the corresponding monthly mean readings of the large Horizontal-force Magnetometer, corrected to the constant temperature 82° Fahr. In correcting the magnetometer readings 0·15 has been adopted as the decrease of reading produced by an increase of 1° of temperature.

Table XIII.

Month.	Mean observed Absolute Horizontal Force.							Corresponding Mean Scale-reading of large Horizontal-force Magnetometer, corrected to Temperature 82°·0.						
	1867.	1868.	1869.	1870.	1871.	1872.	1873.	1867.	1868.	1869.	1870.	1871.	1872.	1873.
January	.....	8·0608	8·0616	8·0655	8·0768	8·0727	8·0750	.....	24·60	24·30	24·77	25·57	25·89	
February	.....	8·0556	8·0688	8·0670	8·0791	8·0743	8·0811	.....	24·61	24·07	24·72	25·61	25·95	10·47
March	.....	8·0597	8·0655	8·0758	8·0774	8·0818	8·0830	.....	24·48	24·29	25·26	25·64	25·96	10·50
April	.....	8·0595	8·0616	8·0697	8·0743	8·0873	8·0856	.....	23·79	24·34	24·90	25·35	26·15	10·64
May	.....	8·0614	8·0547	8·0706	8·0742	8·0876	8·0859	.....	24·32	24·09	25·49	25·80	26·32	10·76
June	.....	8·0688	8·0683	8·0818	8·0790	8·0844	8·0874	.....	24·54	24·84	25·62	25·78	25·79	10·88
July	8·0494	8·0651	8·0695	8·0756	8·0819	8·0811	8·0889	23·53	24·07	24·84	25·21	25·54	25·67	10·93
August	8·0612	8·0490	8·0633	8·0768	8·0808	8·0813	8·0847	23·41	24·15	24·25	25·15	25·42	25·64	10·72
September	8·0508	8·0546	8·0710	8·0700	8·0824	8·0808	8·0828	23·37	23·29	24·31	24·35	25·56	25·39	10·83
October	8·0569	8·0637	8·0646	8·0687	8·0799	8·0753	8·0853	23·32	24·10	24·45	24·56	25·11	25·18	10·99
November	8·0523	8·0659	8·0690	8·0680	8·0757	8·0769	8·0841	24·09	24·51	24·48	24·73	25·37	25·65	11·35
December	8·0593	8·0588	8·0625	8·0787	8·0710	8·0795	8·0849	24·27	24·42	24·74	25·59	25·59	25·38	11·61

Table XIV. corresponds with Table XIII., except that the mean monthly readings deduced from all the hourly observations of the large Horizontal-force Magnetometer are given instead of those which correspond to the times of the absolute observations only; and the values of Horizontal Force are corrected for the difference between the two sets of mean monthly readings, so as to represent the values of the *mean* Horizontal Force for the several months. The scale-coefficient adopted for the large Horizontal-force Magnetometer is $\frac{dX}{X} = \cdot 001488$, or $dX = +\cdot 012$ for an increase of unity in the scale-reading.

TABLE XIV.

Month.	Monthly Mean Absolute Horizontal Force reduced to Monthly Mean Readings of large Horizontal-force Magnetometer.							Monthly Mean Reading of large Horizontal-force Magnetometer, corrected to Temperature 82°·0.						
	1867.	1868.	1869.	1870.	1871.	1872.	1873.	1867.	1868.	1869.	1870.	1871.	1872.	1873.
January	.....	8·0556	8·0584	8·0581	8·0674	8·0668	8·0725	.....	24·17	24·03	24·15	24·79	25·40	
February	.....	8·0491	8·0680	8·0610	8·0681	8·0643	8·0727	.....	24·07	24·00	24·22	24·89	25·12	9·77
March	.....	8·0551	8·0639	8·0654	8·0673	8·0718	8·0757	.....	24·10	24·07	24·39	24·80	25·13	9·89
April	.....	8·0606	8·0552	8·0627	8·0638	8·0770	8·0809	.....	23·88	23·81	24·32	24·39	25·29	10·19
May	.....	8·0578	8·0524	8·0611	8·0658	8·0793	8·0816	.....	24·02	23·90	24·70	25·10	25·63	10·40
June	.....	8·0602	8·0592	8·0708	8·0705	8·0791	8·0809	.....	23·99	24·08	24·70	25·07	25·35	10·34
July	8·0480	8·0617	8·0613	8·0702	8·0735	8·0746	8·0833	23·41	23·79	24·16	24·76	24·84	25·13	10·46
August	8·0593	8·0444	8·0580	8·0672	8·0713	8·0715	8·0822	23·25	23·77	23·81	24·35	24·63	24·82	10·51
September	8·0473	8·0568	8·0619	8·0642	8·0718	8·0744	8·0791	23·08	23·47	23·55	23·87	24·68	24·86	10·52
October	8·0547	8·0573	8·0576	8·0604	8·0752	8·0691	8·0809	23·14	23·57	23·87	23·87	24·72	24·66	10·62
November	8·0487	8·0612	8·0671	8·0630	8·0657	8·0707	8·0793	23·79	24·12	24·32	24·31	24·54	25·13	10·95
December	8·0564	8·0554	8·0582	8·0685	8·0662	8·0752	8·0814	24·03	24·14	24·38	24·74	25·19	25·02	11·32

During part of the month of January 1873 the large Horizontal-force Magnetometer was under readjustment, and the correction had to be deduced partly from its readings before readjustment, and partly from readings of the Horizontal-force Magnetograph taken at the time of the absolute observations. From and after February 1873 the monthly mean readings of the large Horizontal-force Magnetometer were obtained by subtracting from the monthly mean for the five civil hours 6, 10, 14, 16, and 22, the excess, expressed in scale-readings, of the mean force at those hours in the years 1846 to 1872 above the mean force for the twenty-four hours in the same years.

16. *Annual Mean Values and Secular Change.*—The mean value of the Horizontal Force for the epoch October 1, 1870, is 8·0718 or 8·0658, according as the observations are uncorrected or corrected to the mean of the several months.

The following Table shows the mean values, uncorrected and corrected, of the Horizontal Force in each year or half-year from 1867 to 1873, and the corresponding annual increments of Horizontal Force:—

TABLE XV.

Year or Half-year.	As observed.		Corrected to Mean Reading of large Horizontal-force Magnetometer.	
	Horizontal Force.	Annual Increment.	Horizontal Force.	Annual Increment.
1867, July to December	8·0550	[+·0045]	8·0534	[+·0037]
1868, " "	8·0595		8·0561	
1868, January to December	8·0601	+·0049	8·0563	+·0037
1869, " "	8·0650	+·0073	8·0600	+·0044
1870, " "	8·0723	+·0054	8·0644	+·0044
1871, " "	8·0777	+·0025	8·0688	+·0040
1872, " "	8·0802	+·0039	8·0728	+·0063
1873, " "	8·0841		8·0791	
Mean	.....	+·0048	.....	+·0045

The annual increments within brackets, being derived from *half-yearly* means, are allowed only half the weight of the others. The mean secular change of Horizontal Force is thus found to be a yearly increase of ·0048 from the uncorrected observations, or ·0045 from the corrected observations.

17. *Diurnal Inequality at different heights above the ground.*—In Table XVI. a comparison is drawn between the diurnal inequalities of Horizontal Force at corresponding hours, shown by the absolute observations and by the large Horizontal-force Magnetometer.

The temperature- and scale-coefficients used in calculating the numbers in the last column from those in columns 6 to 9 have been already given.

The general result (with which twenty-one half-yearly differences are in agreement, and four of contrary import) is that the diurnal variation of Horizontal Force is, between the hours in question, less in the top room of the Electrometer Tower, at a height of 38 feet above the ground, where the absolute observations were taken, than it is at a height of 6 feet, where the large Horizontal-force Magnetometer is placed; and on the average it is about one fifth less. The average time of the first observation is $12^h\ 22^m$, and that of the second observation $14^h\ 39^m$; and during this interval, which is generally about the same in extent and has nearly the same limits, the mean for the whole year of the regular daily diminution of force is 0·37 of the mean range for the year of the diurnal variation of force, so that we are dealing with a large fraction (more than a third) of the whole diurnal movement. The maximum Horizontal Force of the day occurs about half an hour before the middle of the first observation.

The supposition that most readily suggests itself in explanation of a result of this nature is, that, being derived from observations with instruments of different construction, it is due to error of observation in the one case, or to error in the scale-coefficient or temperature-coefficient employed in the other.

Against the supposition that it is due to error of observation with the Unifilar Magnetometer, it may be urged, first, that it recurs in twenty-one out of twenty-five half-

TABLE XVI.

Half-yearly Period.	Civil Time of First Observation.	Civil Time of Second Observation.	Horizontal Force deduced from First Observation.	Horizontal Force deduced from Second Observation.	Large Horizontal-force Magnetometer at First Observation. Scale-reading.	Large Horizontal-force Magnetometer at First Observation. Thermometer.	Large Horizontal-force Magnetometer at Second Observation. Scale-reading.	Large Horizontal-force Magnetometer at Second Observation. Thermometer.	Excess of First over Second Result. By Absolute Determinations.	Excess of First over Second Result. By large Horizontal-force Magnetometer.
	h m	h m	English Units.							
1867, July to December	12 16	14 44	8·0573	8·0552	23·62	83·4	23·23	84·0	+·0021	+·0036
1868, „ „	12 48	14 49	8·0613	8·0578	23·95	83·7	23·63	84·2	+·0035	+·0030
1869, „ „	12 30	14 38	8·0683	8·0652	24·36	84·2	23·92	84·7	+·0031	+·0043
1870, „ „	12 20	14 40	8·0762	8·0697	25·08	83·1	24·38	83·6	+·0065	+·0074
1871, „ „	12 10	14 29	8·0808	8·0764	25·42	83·7	24·83	84·4	+·0044	+·0059
1872, „ „	12 16	14 37	8·0811	8·0771	25·68	83·3	25·20	84·0	+·0040	+·0046
1873, „ „	12 22	14 55	8·0868	8·0837	11·18	82·6	10·69	83·3	+·0031	+·0046
Mean, „ „	12 23	14 42	.....	.....	.....	.....	.....	.....	+·0038	+·0048
1868, January to June	12 18	14 24	8·0652	8·0632	24·42	83·1	24·09	83·7	+·0020	+·0028
1869, „ „	12 37	14 49	8·0661	8·0611	24·24	84·0	23·74	84·7	+·0050	−·0047
1870, „ „	12 12	14 27	8·0743	8·0703	25·19	83·4	24·55	84·3	+·0040	+·0060
1871, „ „	12 23	14 29	8·0794	8·0741	25·42	85·1	24·83	85·7	+·0053	+·0059
1872, „ „	12 12	14 36	8·0836	8·0790	25·87	82·9	25·01	83·6	+·0046	+·0055
1873, „ „	12 27	14 56	8·0861	8·0825	11·11	83·6	10·49	84·2	+·0036	+·0064
Mean, „ „	12 21	14 37	.....	.....	.....	.....	.....	.....	+·0041	+·0052
1868, Jan. to March and Oct. to Dec.	12 39	14 46	8·0626	8·0592	24·62	81·6	24·29	82·5	+·0034	+·0023
1869, „ „ „	12 43	14 54	8·0678	8·0627	24·56	82·4	24·00	83·2	+·0051	+·0063
1870, „ „ „	12 20	14 31	8·0736	8·0679	25·21	81·9	24·59	82·8	+·0057	+·0061
1871, „ „ „	12 18	14 27	8·0790	8·0743	25·55	83·0	24·99	83·9	+·0047	+·0050
1872, „ „ „	12 13	14 34	8·0789	8·0742	25·63	81·1	25·11	82·1	+·0047	+·0044
1873, „ „ „	12 20	14 53	8·0850	8·0819	11·67	81·7	11·09	82·7	+·0031	+·0050
Mean, „ „ „	12 25	14 41	.....	.....	.....	.....	.....	.....	+·0044	+·0047
1868, April to September	12 28	14 28	8·0638	8·0617	23·75	85·1	23·44	85·4	+·0021	+·0031
1869, „ „	12 24	14 33	8·0666	8·0636	24·02	85·9	23·65	86·4	+·0030	+·0036
1870, „ „	12 12	14 32	8·0769	8·0721	25·07	84·6	24·35	85·1	+·0048	+·0078
1871, „ „	12 14	14 31	8·0811	8·0762	25·26	85·8	24·67	86·3	+·0049	+·0064
1872, „ „	12 15	14 39	8·0857	8·0819	25·61	85·1	25·08	85·5	+·0038	+·0055
1873, „ „	12 28	14 56	8·0878	8·0842	10·69	84·2	10·17	84·7	+·0036	+·0053
Mean, „ „	12 20	14 37	.....	.....	.....	.....	.....	.....	+·0037	+·0063

yearly comparisons; and secondly, that the probable error of a single weekly determination (that is, of the mean of the first and second observation) being $\pm$·0043 (see paragraph 19), that of the mean difference, for six and a half years, between the first and second observations will be less than $\pm$·0005 (or $=\pm 0043 \div \sqrt{\frac{338}{2}} \times \sqrt{2}$), a quantity which is less than half the magnitude of the difference that the error is supposed to explain. And if it were due to erroneous allowance for temperature of the large Horizontal-force Magnetometer, it ought to be small when the diurnal range of temperature is small, and large when the range is large; whilst, in fact, the difference in question is only ·0003 in the half-year October to March, when the range of temperature is large, and is ·0016 in the half-year April to September, when the range of temperature is small. At the same time the range of the diurnal variation of Horizontal Force is nearly the same throughout the year, its value for the half-year October to March being a fourteenth greater than for the half-year April to September, and its mean value for the year, as shown by the large Horizontal-force Magnetometer, is ·00166 of the whole force. It remains, therefore, if the result be an instrumental one, that the scale-coefficient adopted for the large Horizontal-force Magnetometer must be supposed to be one fourth of itself in excess of the truth: this the writer cannot think possible, and he hopes soon to have the opportunity of submitting to the judgment of the Royal Society evidence (in connexion with a general discussion of the observations with this instrument) which will completely set aside such a supposition.

If the result be admitted as a true magnetic phenomenon, it suggests the attribution of a very considerable magnetic influence to the state of the medium intervening between the upper and lower places of observation, in such a way that when the air is of equable temperature and almost uniformly moist throughout, the variations of force are nearly alike above and below, whilst in the dry months of the year there is a very considerable diminution of daily change of force with increase of height. The writer readily admits that such attribution should not rest upon a result of observations taken at a single station only.

18. *Annual Variation.*—In Table XVII. are shown the means for each month, in the period of six and a half years, of the values of Horizontal Force, corrected to the mean monthly reading of the large Horizontal-force Magnetometer; also the corrections for secular change, at the rate of +·0045 per year, to reduce those means to the common epoch, October 1, 1870, and the same means cleared of secular variation; and, further, the excess of each of the corrected monthly values above the mean value for the year, the last series of numbers representing the annual variation of Horizontal Force.

TABLE XVII.

Months	Jan.	Feb.	March.	April.	May.	June.	July.	August.	Sept.	Oct.	Nov.	Dec.	Year.
Mean horizontal force	8·0631	8·0639	8·0654	8·0664	8·0663	8·0701	8·0675	8·0648	8·0651	8·0650	8·0651	8·0650	...
Correction for secular change ...	+9	+6	+2	−2	−6	−9	+9	+6	+2	−2	−6	−9	...
Corrected to epoch Oct. 1, 1870 ...	8·0640	8·0645	8·0656	8·0662	8·0657	8·0692	8·0684	8·0654	8·0653	8·0648	8·0645	8·0650	8·0658
Annual variation ...	−·0018	−·0013	+·0008	+·0004	−·0001	+·0034	+·0026	−·0004	−·0005	−·0010	−·0013	−·0008	...

The annual variation exhibits a semiannual inequality in which the horizontal force is, during the months March to August, ·0011 greater than the mean of the year, and during the months September to February ·0011 less. The quarterly means that give the greatest difference are as follows:—

February to April	·0000
May to July	+·0020
August to October	−·0006
November to January	−·0013

Without applying any corrections for secular change, the means of the values of Horizontal Force in Table XVII., for January and December, February and November, &c., will all correspond to the same epoch, October 1, 1870. Such means are compared below both for the uncorrected observations and for the observations corrected to the mean of each month.

TABLE XVIII.

Months.	Uncorrected.		Corrected.	
January and December	8·0697	8·0701	8·0645	8·0645
February and November.....	8·0706		8·0645	
March and October.....	8·0722	8·0719	8·0657	8·0657
April and September	8·0716		8·0657	
May and August	8·0717	8·0736	8·0655	8·0671
June and July	8·0755		8·0688	
April to September	.....	8·0729	.....	8·0667
October to March	.....	8·0708	.....	8·0649

Both sets of numbers indicate a small semiannual inequality, in which the force is about a four-thousandth of itself greater in the half-year April to September than in the half-year October to March; and the four-monthly means show that the force passes through its mean value in the months March, April, September, and October nearest to the equinoxes; and thence, of necessity, the maximum occurs in the months May to August, about the summer solstice, and the minimum in the months November to

February, about the winter solstice. The difference of range of the four-monthly means, uncorrected and corrected, is doubtless a consequence of the uncorrected values having reference to the mean interval from $12^h\ 22^m$ to $14^h\ 39^m$, whilst the corrected values have reference to the mean of the twenty-four hours.

Whilst, however, recording this result as that which the absolute observations are capable of yielding, the writer does not claim for it any great confidence; for the probable error of an observation is considerably greater than the monthly differences which have been obtained as representing the annual variation; and consequently it is only by combining together the observations of a number of years that the influence of errors of observation can be expected to be practically eliminated, and half the period of six and a half years seems not to be sufficient for this purpose; for when the observations are separated into two groups (of three and a half years and three years) the annual variations yielded are of totally different character.

19. *Probable Error.*—The probable error of a single weekly determination of Absolute Horizontal Force has been computed separately for July to December 1867 and for the year 1868. This has been done independently from all the complete observations except those of July 2 to 27, 1867, and for all, with the further exception of those of August 21, 1867, and April 8 and 15 and August 19, 1868, which give results that are evidently erroneous, far beyond the range of observational error. The observations were all reduced to the constant reading 24·27, at temperature 82°, of the large Horizontal-force Magnetometer, allowance being further made for the loss of strength of the magnet of that instrument; and the differences being then taken between each corrected determination and the mean of all, the probable errors were calculated from these differences by the method of least squares. The rate at which allowance was made for the loss of strength of the magnet was ·00015 of the whole per annum (see 'Introduction to Bombay Observations,' 1864, page xvi). The probable errors found are as follows:—

TABLE XIX.

Period.	Including abnormal values.		Excluding abnormal values.	
	English Units of Force.			
	Of a single weekly determination.	Of the mean of all the determinations.	Of a single weekly determination.	Of the mean of all the determinations.
July to December 1867	±·0053	±·0011	±·0043	±·0009
January to December 1868	±·0067	±·0009	±·0043	±·0006

The remaining observations of 1869 to 1873 being of about the same quality as those of 1868, will have about the same probable error.

The maximum probable error (that of the moment of inertia of the vibration-magnet)

of the constants used in reductions of the Horizontal-force observations has about the same effect ($\pm$·0006) as the smallest of the above determinations, which have reference to observational errors only.

IV. *Total Force.*

20. With the following data:—

Dip for epoch 1st October, 1868	=19° 4′·2
Secular change of Dip per annum	=+1′·9
Semiannual inequality of Dip:—excess from April to September above the mean of the year . . .	=+0′·3
Horizontal Force for epoch 1st October, 1870 . . .	= 8·0658
Secular change of Horizontal Force per annum . .	=+ ·0045
Semiannual inequality of Horizontal Force: excess from April to September above the mean of the year	=+ ·0009

We find

Dip for epoch 1st January, 1871	=19° 4′·2
	+2·25×1′·9=19° 8′·5
Horizontal Force for epoch 1st January, 1871 . . .	$=8{\cdot}0658+\frac{{\cdot}0045}{4}$
	=8·0669

And by the formula $R=\frac{X}{\cos\theta}$, where R represents the Total Force, X the Horizontal Force, and θ the Dip:—

Total Force for epoch 1st January, 1871	= 8·5391

And by the formula $dR=\frac{dX}{\cos\theta}+R\tan\theta\, d\theta$:—

Secular change of Total Force per annum	=+ ·0064
Semiannual inequality of Total Force: excess from April to September over mean of the year . .	=+ ·0012

21. *Annual Variation.*—In the annual variation of Total Force, derived by the formula last given from those of Dip and Horizontal Force in Tables III. and XVII., the monthly excesses above the yearly mean are, for January to December respectively, as follows:— −·0025, −·0015, +·0008, +·0008, +·0004, +·0039, +·0029, −·0001, −·0004, −·0011, −·0015, and −·0015; and the quarterly means which give the greatest differences are:—February to April, ·0000; May to July, +·0024; August to October, −·0005; and November to January, −·0018.

V. *Absolute Magnetical Results.*

Collected together.

TABLE XX.

Magnetic Element.	Epoch.	Value at epoch.	Value at common epoch, 1st January, 1871.	Secular change per annum.	Semiannual inequality: excess of April to September over mean of year.	
Declination	1st October, 1870 ...	0° 46′ 32″	0° 50′ 8″	+1′ 48″	−0′ 1″	
Dip.....	1st October, 1868 ...	19 4·2	19 8·5	+1·9	+0·3	
Horizontal force ...	1st October, 1870 ...	8·0658	8·0669	+ ·0045	+ ·0009	Foot-grain-second units.
Do. ...	.....	.....	3·7195	+ ·0021	+ ·0004	Metre-gramme-second units.
Total force.....	.....	.....	8·3391	+ ·0063	+ ·0012	Foot-grain-second units.
Do.	.....	.....	3·9372	+ ·0029	+ ·0006	Metre-gramme-second units.

IV. *On the Structure and Relations of the Alcyonarian* Heliopora cærulea, *with some Account of the Anatomy of a Species of* Sarcophyton, *Notes on the Structure of Species of the Genera* Millepora, Pocillopora, *and* Stylaster, *and Remarks on the Affinities of certain Palæozoic Corals. By* H. N. Moseley, *M.A. Oxon., Naturalist to the 'Challenger' Expedition. Communicated by Professor* Wyville Thomson, *F.R.S., Director of the Civilian Staff of the 'Challenger.'*

Received September 28,—Read November 25, 1875.

Introduction.

Having undertaken the examination of the Deep-sea Corals dredged by the 'Challenger' during her voyage, my attention was naturally directed to the study of the structure of corals generally. The Milleporidæ, both because of their peculiar tabulate structure and relations to fossil forms, and because of Prof. Agassiz's well-known determination of them as Hydroids and not Actinozoa, seemed to offer the most interesting field for investigation; and I accordingly commenced the examination of their structure very early in the cruise of H.M.S. 'Challenger' in April 1873, at Bermuda, where *Millepora alcicornis* occurs in great profusion.

I made a number of preparations and made out some points in the anatomy of this species, but found the subject to be so difficult that I put the matter aside to be further examined on reaching England. In the beginning of 1875, however, I obtained specimens of *Heliopora cærulea* in the living state at Zamboangan, and on examining these found to my astonishment that *Heliopora* was an Alcyonarian. I therefore during subsequent voyages made as complete an examination as possible of this species, and examined for comparison with it the structure of another Alcyonarian, a species of *Sarcophyton* dredged in shallow water amongst the reefs of the Admiralty Islands. I examined further the structure of a species of *Millepora* obtained at Zamboangan; and I also examined a *Pocillopora* found at the same locality, and a species of *Stylaster* dredged in 500 fathoms off the Meangis Islands. The results form the substance of the present paper.

Recent Literature concerning Tabulate and Rugose Corals and Alcyonarians &c.

I am able to refer to very few original papers relating to the present subject, but have gathered the following from the more general works available on board the 'Challenger.' It is hoped that allowance will be made for the peculiar conditions under which this paper is written.

M. Milne-Edwards (Hist. Nat. des Coralliaires, Paris, 1860, t. iii. p. 224) forms the

family Milleporidæ to include a series of genera, amongst which *Millepora* and *Heliopora* are the only recent ones, whilst he classes the Pocilloporinæ as a subfamily of the Favositidæ, together with the Milleporidæ and Seriatoporidæ, under his section of the Madreporaria Tabulata. The section is characterized by having the corallum composed essentially of a much developed mural system, with the visceral chambers divided into a series of stories by complete diaphragms or transverse floors, the septal arrangements being rudimentary or represented by trabeculæ, which have a greater or less extension in the intertabulate spaces. In his description of the Milleporidæ (*l. c.*) M. M.-Edwards refers to Prof. Agassiz's then recent paper, entitled "Les Animaux des Millépores sont des Acalèphes Hydroides et non des Polypes," Bibl. Univ. de Genève, Arch. des Sci., Mai 1859, t. v. p. 80, to the following effect:—"At the moment of sending this chapter (on the Madreporaria Tabulata) to the press, we learn that Prof. Agassiz has studied the mode of the organization of the soft parts of the Milleporidæ, and has proved that these Zoophytes are not corals, but Hydroid Acalephs very nearly related to the Hydractiniæ. Prof. Dana shares the opinion of Prof. Agassiz; and Agassiz believes that the Favositidæ, as well as all other species of which the septa are not continued vertically, ought to be considered strangers to the class of corals. But the facts on which he grounds his opinion are not as yet sufficiently ascertained for us to be able to form a critical opinion of their value; and until more ample information is received, we shall continue to rank the polyps in question according to the method adopted in our former works."

Professor L. Agassiz, in his 'Contributions to the Natural History of the United States,' vol. iii. plate 15, figured the animals of *Millepora*. He places *Millepora*, *Heliopora*, *Seriatopora*, *Pocillopora*, the whole of the Tabulate and Rugose Corals, with the Hydroid Acalephæ. The principal distinction between these sections and true polyps relied on by Agassiz, as quoted in Bronn's 'Klassen und Ordnungen des Thierreichs' (Actinozoa, 1860, p. 45, note), is as follows:—"True polyps should have unbroken septa throughout the whole calicle, with only separated horizontal partitions between them. On the other hand, the hydroid Favositidæ had complete horizontal partitions between interrupted septa." Professor Agassiz hoped that deep-sea dredgings would produce additional evidence concerning the affinities of *Millepora*, and genera connecting more closely the Rugosa and Tabulata with one another and with the Acalephæ in the shape of branching Heliopores and the like. (A letter concerning Deep-sea Dredgings, addressed to Prof. Benjamin Pierce, Superintendent of the United States Coast Survey, by Louis Agassiz. Cambridge, Mass., Dec. 1871). Since Agassiz's observations on *Millepora* were published, no one has made any examination of the structure of the soft parts of any of the members of the Tabulata, with the exception of Prof. Verrill, who has examined a *Pocillopora* and found it to be a true Zoantharian polyp with twelve septa and twelve tentacles (Ann. & Mag. Nat. Hist. 1872, vol. ix. 4th series, p. 355, from Silliman's 'American Journal,' 1872, vol. iii. pp. 187–194, "On the Affinities of Palæozoic Tabulate Corals with Existing Species").

Professor Verrill, in the paper above quoted, as he has done before, combats the conclusions of Prof. Agassiz, that the whole of the Tabulata belonged to the hydroid polyps. This fact, he says, has only been proved for the Millepores: the remaining Tabulata should be joined with the true polyps, with which their relations are very near and intimate. The transverse partition-walls, the presence of which was held by Milne-Edwards and Haime as a characteristic distinction, are structures of a very low order, that occur *in widely different forms*, and are only brought about by the simultaneous emptying of the generative products from the radial chambers. Where the emptying is not thus periodically simultaneous, a separate transverse septum is formed in each of the chambers shutting off the space thus become vacant. True tabulæ are found not only in *Millepora* and *Pocillopora*, but in *Cœlastræa*, *Alveopora*, and *Asteropsammia*. *Columnaria* is, apparently, closely allied to *Cœlastræa*, *Favosites* to *Alveopora*, *Porites*, &c. *Heliopora* being shown to be an Alcyonarian, tabulæ are proved to be present in forms still more widely different than is shown to be the case by Prof. Verrill. The relation of *Favosites* and *Columnaria* appears now in a different light.

The opinions expressed concerning Professor Agassiz's relegation of the Tabulate and Rugose Corals to the Hydroids have been various.

Professor Allman, in his 'Monograph of the Gymnoblastic or Tubularian Hydroids' (London, published for the Ray Society by Robert Hardwicke, 192 Piccadilly, 1871, page 3), refers to Professor Agassiz's opinion on the subject as published in his 'Contributions to the Natural History of the United States.' He considers that since we are entirely ignorant of the generative system of the Milleporidæ, it is much safer to wait for such verification as may be expected from further researches. He hesitates to include amongst the Hydrozoal orders the Tabulate and Rugose corals. Professor Allman (Quart. Journal Micr. Science, vol. lxii. pp. 394, 395) considers *Edwardsia* to occupy an intermediate position between Zoantharian and Alcyonarian polyps, and to be comparable with the extinct Rugosa, to which it corresponds in the numerical law of its body-segments.

Count Pourtalès (Illustrated Catalogue of the Museum of Comparative Anatomy at Harvard College, Cambridge, Mass.: No. iv. Deep-sea Corals, p. 56) places the Milleporidæ with the Hydroids. He remarks, "No observations have been made on *Millepora* since Professor Agassiz's first announcement of the affinities of the Millepores with the Hydroid polyps twenty years ago. The polyps of *Millepora* are very difficult to observe, both because of their small size, and because they are killed by the shortest contact with air; when obtained expanded, they contract on the slightest shake of the vessel containing them. I have succeeded but once in having a good view of one of the larger polyps of *Millepora alcicornis* in company with Professor Agassiz. It differed from the figure in the 'Contributions to the Natural History of the United States,' vol. iii. plate 15. fig. 1, in being comparatively shorter and having larger tentacles, or rather *tentacular masses* studded with lasso cells five in number instead of

four. The mouth was not seen very distinctly, but appeared to be a transverse slit in the middle of the disk. It remained expanded but a short time."

Pourtalès places the genus *Pliobothrus* amongst the Milleporidæ. The Rugosa he places at the end of the true corals. He has by the examination of the *Lophophyllum proliferum* (M.-Edwards and Haime) come to the conclusion that the tetrameral arrangement claimed for the Rugosa is only apparent, there being originally six primary septa. The coral was examined by cutting successive transverse sections. Such a section from the tip of *Lophophyllum proliferum*, representing the youngest stage, shows six primary septa and six interseptal spaces placed symmetrically on two sides of a vertical plane and unequally developed. By unequal development of additional septa in further development (investigated by the examination of sections successively nearer to the margin of the calicle) the seeming tetrameral arrangement is produced. Pourtalès refers to papers on the subject by Römer and Lindström, and cites L. Ludwig (H. von Meyer's 'Palæontographica,' vols. x. & xiv.) as having shown the same facts and come to like conclusions concerning the affinities of the Rugosa, publishing his results before Pourtalès.

A. Kunth (Zeitschrift der deutsch. geol. Ges. xxi. Heft 3) is also cited by Pourtalès. Kunth has examined the law of growth of the Rugosa chiefly by the consideration of the successive development of the costæ. He still adheres to the tetrameral primary division, from want, in the opinion of Pourtalès, of having examined individuals of very young age and hence great simplicity.

Kunth is further quoted in Leuckart's Jahresbericht, 1870–71, p. 192, as finding the analogue of the operculum of Zoantharia Rugosa in the folds of skin described by Milne-Edwards as occurring in *Cryptohelia pudica* "trotz der fehlenden Verkalkung." There must be some error here. Surely Kunth refers to the calcareous lamina projecting in front of the mouth of the calicle of *Cryptohelia* springing from its margin.

Kunth (Zeitschrift der deutschen zoolog. Gesellschaft, 1870, p. 81; Lindström, Œfvers. Kongl. Vetensk.-Akad. Förhandl. Bd. xxvii. pp. 922–926), the first discoverer of the opercular apparatus of Rugosa, compares the opercula to the skeletal structures of certain Primnoas, especially *Primnoa lepadifera*, *Paramurina placomus*, and *Cyathophyllum Loveni*. *Goniophyllum pyramidale* had four valves at the anterior end placed in pairs opposite one another, and only differing in that one of them is larger than the others. This larger one is the homologue of the one opercular valve of *Calceola* and *Rhizophyllum*.

Prof. Claus (Grundzüge der Zoologie, 3te Auflage, 1874, p. 226) places the Milleporidæ with the Hydroids. The Rugosa he considers should be separated as a third order of Anthozoa equivalent to the Alcyonaria and Zoantharia, and remarks on the relations between Rugosa and Hexactinia shown by the developmental history of the latter.

Saville Kent (Ann. & Mag. Nat. Hist. 1870, vol. vi. pp. 384–387) describes *Favositi-*

pora Deshayesii as an existing coral closely allied to the palæozoic genus *Favosites*. The coral has abundant complete horizontal partitions and closely resembles *Alveopora fenestrata*; it connects the Favositidæ and Poritidæ, and is a new proof that the Tabulates belong to the Anthozoa and not to the Hydroids.

Prof. P. Martin Duncan ("A Description of the Madreporaria dredged up during the Expeditions of H.M.S. 'Porcupine' in 1869 and 1870," Trans. Zool. Soc. London, vol. viii. part 5, p. 335) describes *Guynia annulata* as a recent Rugose coral. In this coral there is no endotheca. In three specimens there were evidences of a hexameral septal arrangement. One had an octameral arrangement at the base and a hexameral at the calicular margin. This specimen is believed to illustrate the formation of the Neozoic type from the Rugosa. Prof. Duncan has treated on the affinities of *Guynia* with *Haplophyllia* in a paper in Phil. Trans. Roy. Soc. 1872, which paper I have not seen. *Haplophyllia paradoxa* is another recent supposed representative of the Rugosa from the deep sea described by Pourtalès in the 'Bulletin of the Museum of Comparative Zoology, Harvard Coll. Camb. Mass.' no. 7, and also in his work on deep-sea corals already cited. Unfortunately the soft parts of neither *Guynia* nor *Haplophyllia* were obtained for examination.

The latest paper treating on the classification of corals to which I have access is by M. G. Dollfus ("Observations critiques sur la classification des Polypiers paléozoïques," Comptes Rendus de l'Acad. des Sciences, t. lxxx. no. 10, 15 Mars 1875, pp. 681–683). M. Dollfus classes certain of the Tabulata, the Héliolitiens (*Heliolites*, *Lyellia*, *Propora*), with the modern Milléporiens (*Heliopora*, *Millepora*, *Seriatopora*), connecting them by the Pocilloporiens (*Pocillopora*, *Axopora*, *Polytremacis*) most unfortunately, since *Pocillopora* is a Hexactinian. He considers all these genera to be Hydroids. The Chætétiniens (*Stellipora*, *Monticulipora*, *Chætetes*, *Cœnites*, *Dania*, *Beaumontia*, *Labechia*, *Dekaya*) he considers to be Bryozoa allied to the Jurassic *Heteropora* and Cretaceous *Radipora*. The group of Favositiens (*Alveolites*, *Favosites*, &c.) presents, as he considers, relations with the tubuline Bryozoa, the Cyclostomata.

It will be seen from the above abstracts that the relations of the Tabulate and Rugose Corals are in a very uncertain condition, and that there is very wide difference of opinion on most important points. It is hoped that some light will be thrown on the subject by the present paper.

In addition to the authors cited above, the following papers and works will be referred to in the sequel (they have mostly been accessible only in abstract):—

Quenstedt . . . . Handbuch der Petrefactenkunde. Tübingen, 1867.

Metschnikoff . . . On the Development of *Kalliphobe* (Busch). Bullet. Acad. Impér. St. Pétersbourg, t. xv. pp. 502, 503.

Lacaze-Duthiers . . Hist. de Développement des Coralliaires. Arch. Z. expér. i. pp. 289–296.

Sars . . . . . On the Polyps of *Allopora oculina*. Forh. Selsk. Chr. 1872, p. 115.

Prof. A. Schneider and M. Rötteken. On the Structure of Actiniæ and Corals. Sitzungsbericht der oberhessischen Gesellschaft für Natur- und Heilkunde. 1 March, 1871.

Kölliker . . . . Anatomisch-systematische Beschreibung der Alcyonarien. Abh. der sensk. naturf. Gesell. Frankfurt, 1870. To this work I was able to make a short reference at Yeddo through the kindness of Dr. Hilgendorf.

Kölliker . . . . On the frequent occurrence of Vegetable Parasites in the hard tissues of Animals. Quart. Journal of Microscopical Science, 1860, vol. viii. p. 171.

Dr. Carpenter . . . On the Structure of the Shells of Molluscous and Conchiferous Animals. Trans. Microscopical Society, 1844, ser. 1, vol. i. p. 123.

Methods.—The corals and the *Sarcophyton* examined were hardened in absolute alcohol, being placed in it in the living condition. Portions of them were subsequently decalcified in weak hydrochloric acid, imbedded in wax in the usual manner, and sections were then prepared from them. The sections were examined partly in glycerine, partly in Canada balsam, after being rendered transparent by means of oil of cloves. Some sections were stained with carmine. Some portions of *Heliopora* were placed whilst living in a solution of chromic acid, and slowly decalcified whilst in the solution by the addition of a few drops of hydrochloric acid from time to time; these yielded some results which were not obtainable from specimens hardened in alcohol and more rapidly decalcified. Further sections of small area were forcibly cut from the undecalcified hardened corals in order to show the relations of the hard parts to the soft, and separate polyps were removed from their calicles with the point of a scalpel and examined whole in glycerine. Portions of the tissues of *Heliopora* were also observed in the fresh condition.

For examination of the structure of the hard calcareous tissues, fine sections were prepared by grinding in the usual manner.

Account of the structure of Heliopora cærulea.

Heliopora cærulea was found growing in abundance on the reefs fringing the shore of the small island of St. Cruz Major, which lies opposite the harbour of Zamboangan, Mindanao, Philippine Islands. The coral grew in about two feet of water at low tide. It has a uniform light chocolate-colour when fresh and living. Although I transferred portions of the living coral to a glass vessel under water so that they never came in contact with the air, I did not succeed in getting the polyps to expand; and I have

not seen them in that condition, although directly the coral was left at rest a swarm of a species of *Leucodora*, closely resembling *Leucodora nasuta*, which infests the coral and perforates it all over, expanded themselves at once. Most unfortunately I hardened in spirits portions of *Heliopora* taken from only one colony, as I did not suspect that the animal would prove to form unisexual colonies. This colony proved to be female; and hence I have not seen the male generative organs of *Heliopora*. The only reference to the structure of the soft parts of *Heliopora* which I have found is a statement of Quenstedt (*l. c.* p. 795), that Quoy says that the animals of *Heliopora* have more than twelve rays.

Structure of the Corallum of Heliopora cærulea*.

The genus *Heliopora* was formed by Blainville (Manuel d'Actin. p. 392). It is thus characterized by Milne-Edwards, *l. c.* p. 230:—"Corallum massive, lobulate, and rising in a tuft. Cœnenchym very abundant, and presenting at its surface a great number of rounded pores, disposed with regularity and separated by projecting papilliform grains. These grains are formed by the upper extremities of an equal number of cylindrical and vertical beams, which shut in tubuliform spaces, open above, and divided from space to space by cross partitions. Calicles circular. Septa very little developed, but distinct and 12 in number. Horizontal floors present and well developed. The genus is remarkable for its alveolar appearance and the tubular structure of the parenchym."

The coral is figured by M.-Edwards, *l. c.* pl. 1. figs. 3*a*, 3*b*, 3*c*. A drawing of the growing tip of a frond, much enlarged, will be found on Plate 9. figs. 16 and 17 of this paper. The following points require to be remarked concerning the structure of the corallum. The papilliform eminences described by M.-Edwards as covering the surface of the corallum spring from the points of apposition of the walls of several of the cœnenchymal tubes, very usually from the point of meeting of the mouths of four tubes (Plate 9. fig. 17); here the hard tissue consists of a thickened vertical beam of calcareous matter, from which thin lamellar-like processes are given off, which form the walls between two contiguous tubes by crossing to join similar processes from the thickened beams situate at the point of apposition of these two tubes with the pair next succeeding them in the same direction. The narrow summits of the thin laminæ forming the sides of the tubes fall short in their centres, by a considerable distance, of the level of the thickened masses from which they spring, but are rather excavated or hollowed out at these spots; and it is across these excavations in the laminæ that the deep system of canals passes in the fresh condition of the animals, by means of which the cavities of the tubes and polyps communicate freely with one another. The structure of the cœnenchym of the coral might be better described by saying that it consists of a series of tubes of circular

* I regret extremely that I am unable to refer to MM. Milne-Edwards and Haime's papers, "Recherches sur les Polypiers," Ann. Sc. Nat. iii., ix., xvi.

section of nearly uniform diameter, closely packed side by side more or less in regular rows, with their walls where touching fused together, and the spaces necessarily resulting from such an arrangement at the meeting-points of every three or four contiguous tubes filled in with calcareous matter, forming rods or beams of hard tissue, which are elevated above the margins of the tubes into papilliform prominences. MILNE-EDWARDS distinguishes between the tabulæ of the cœnenchymal tubes and those of the calicles, calling the first "traverses," the second "planchers horizontaux;" but these are essentially similar structures. Though twelve is a common number for the projecting plications of the margin of the mouth of the calicle, the number is very variable; 11, 13, 14, even 15 or 16 of these so-called septa are to be counted not uncommonly. In the enlarged figure of a calicle (fig. 17, Plate 9) Mr. WILDE has drawn fifteen. The plications become less numerous at a slight depth in the calicle, and often here are only eight in number, with a mesentery of the polyp passing to each internal projection.

The fine structure of the hard tissue of *Heliopora* is in many respects similar to that of the coralla of Hexactinian corals. It is composed of doubly refracting calcareous matter, which has half-crystalline, half-fibrous structure. On transverse section, fig. 4. Plate 8, it is seen to be made up of a series of systems of radiating fibres, *i. e.* areas of calcareous tissue showing a radiate fibrous structure. In each system the fibres radiate from a central axis and diverge to fuse at the margin of the system with the margins of the contiguous systems, a suture-like line being often observable where two systems join. The fibres are dispersed more or less in laminæ which overlap one another. The radial fibrous structure is to be seen only in thin slices or fragments of the coral viewed by transmitted light. The fracture of the coral is irregular and crystalline. The central axes of the systems correspond to the centres of the vertical beams already described, which are prolonged above on the surface of the coral into papilliform projections. In a vertical section of the corallum (fig. 11, D, Plate 9) these axes are seen to take a vertical course within the beams and branch beneath the newly formed buds of the cœnenchym. The fibres are seen starting from the axes, spreading right and left from them throughout the tissue, with a uniform inclination upwards (*i. e.* towards the surface of the corallum). In the plates forming the sides of the tubes (B, fig. 11, Plate 9) the sutures between the fibres meeting one another at an angle from the two systems are well marked. The appearance of a portion of the hard tissue, as seen under a high power, is shown in fig. 12, Plate 9, where the appearance of the overlapping laminæ is to be remarked. In the corallum of *Pocillopora* definite rod-like prisms with polygonal ends are to be seen to exist by viewing these structures end on; in *Heliopora* such a definite structure apparently does not occur*.

* The radiating components of the hard tissue are here spoken of as fibres to distinguish them from these well-marked prisms of which the hard tissue of *Pocillopora* is composed. The exact nature of the radial striæ seen in the tissue of the *Heliopora* I do not understand; they seem to represent spaces between variously shaped splinters, as it were, of hard matter arranged so as to form laminæ.

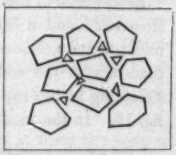
The transverse partitions in the tubes and calicles give evidence in their structure that they are later additions to the inside of an already formed tube. They are not merely transverse floors, but flat-bottomed cups of tissue fitted inside the old tube, and thus narrowing its bore considerably in the region where they become formed. The old boundary line of the tube below the tabula can nearly always be traced, continuing its course for some distance beyond and above the tabula (Plate 9. figs. 11, 15). The tabulæ of the cœnenchymal tubes seem in all respects identical in structure with those of the calicles.

The structures which form the centres from which the systems of hard tissue radiate have been called axes. They have the appearance of being canals in the hard tissue; but this appearance seems to be fallacious. They appear to represent the points of junction of the walls of the opposed cœnenchymal tubes where imperfect fusion has taken place between these walls, and the interspace has been filled with amorphous rather than fibrous calcareous matter. In some cases in transverse sections these axes appear as elongated spaces between the adjacent tubes, rather than central canals. The appearance of these axial structures is accurately represented in Plate 8. fig. 4. There is always a somewhat opaque, fine, granular area around them, which shows often a series of concentric zones.

The opaque tissue surrounding the axes is continued into the projecting points at the surface of the coral. These points sometimes show a banded appearance, as if they had received in growth successive caps of hard tissue (Plate 9. fig. 11, P).

On the Growth of the Corallum of Heliopora cærulea.

If a rapidly growing tip of a frond of *Heliopora cærulea* be carefully protected from injury and macerated in potash, the appearance of its corallum will be that given in Plate 9. fig. 16. The tissue at the actual tip is seen to be much more delicate and spongy-looking than in the older parts. It consists here superficially of an aggregation of thin-walled cells, which are mostly multiangular in outline at their mouths, sometimes hexagonal, often pentagonal, often with curved sides, assuming these various forms apparently from mutual appressure in growth. In the angles where the walls of the adjoining cells meet are the commencements of new cells, which in their very earliest stage are often triangular in superficial outline (see diagram). Amongst this mass of polygonal cells new calicles are developed by the arrest in growth of one or more cells after they have reached a certain small height, which cell or cells form a central floor to the calicle. All around this central floor, contiguous, deeper, older cells form a circular zone. Their inner walls, *i. e.* those nearer to the centre of the growing calicle, cease to grow, and only their outer ones continue to develop; and these being fused together form the lateral walls of the calicle,



and the plications in the wall of the fully formed calicle are to a great extent* the result of this peculiar mode of growth. This will be understood by reference to Plate 9. figs. 16 & 17, and also to Plate 9. fig. 15, where at B a section of a newly formed calicle is given.

In a newly formed calicle, thus, the cavity is comparatively shallow in the centre, but prolonged at the bottom all round into a series of tubular offsets. Into these tubular offsets the mesenterial filaments hang down in the fresh condition of the animals. On further simple growth the tube of the calicle becomes elongated, and receives a new uniform bottom in the shape of a tabula. As the calicle approaches maturity, the cells immediately around it become nearly occluded at their mouths by increased development of calcareous matter at its margin. In older parts of the corallum the mouths of all the tubes are rendered very small by the excessive thickening of their walls and of the beams of hard tissue bearing the projecting points. On a quickly expanding frond of the coral the mouths of the series of cœnenchymal tubes, which are rapidly increasing, are disposed in almost regular straight or curved lines radiating towards the points of extension. In this condition the lateral walls of each line of cells frequently fuse, becoming common to the line and more developed and prominent than the transverse ones, and thus come to form long, delicate ridges with projecting points on their edges, running almost parallel to one another, and with troughs between them. In these troughs calicles may arise, being most irregular in outline at first, but gradually becoming shapely by taking in surrounding cells. In some cases the point-like prominences at the margins of the walls of the cells included within a newly formed calicle may be seen at the bottom of the calicle, maintaining a disposition parallel to that of the trough in which the calicle is formed.

These lines of calicles may be termed lines of growth. The calicles show a more or ss marked disposition in transverse curves, cutting these lines at right angles.

The development of the *Heliopora* colony probably takes place somewhat as repre sented in Plate 9. fig. 15. The original calicle (A) increases in length and forms successive chambers, A′, A″, A‴, A⁗, by developing tabulæ. It gives off a series of buds from its margin, which become elongate tubes divided into compartments in the same way, and in their turn give off buds. New calicles are formed as at B in the figure.

Formation of the Hard Tissue.

Everywhere in the living portions of the coral applied to the surface of the hard tissues is found a layer composed of elongate connective-tissue cells. The cells are nucleate and are finely granular in appearance, and are frequently drawn out into fine filaments at the ends. These cells occur only in connexion with the hard tissue, excepting in the superficial layer of the mesoderm beneath the epidermis, Plate 9. fig. 10. In the median plates of the mesenteries, for example, where no calcareous

* Not entirely, sometimes two plications can be seen corresponding to one lateral tube only in a young calicle.

matter is formed, they are wanting, and homogeneous connective-tissue alone present. It seems hence almost certain that they are the instruments of formation of the calcareous tissue. The newly formed and growing points of the corallum yield much more organic remains after treatment with acids than the older portions. If one of these small points, after having been treated with a strong solution of potash, be examined under the microscope, it will show apparently no trace of consisting of any thing but the usual doubly refracting calcareous matter. If it be then slowly decalcified, an investing layer of finely fibrous tissue is gradually brought into view as the lime is removed. The fibrous tissue seems to form an investment to the hard part, or rather to be present only in its peripheral regions, the central part of the piece of corallum appearing to be free, or almost so, from contained fibrous structures, and thus to be more rapidly attacked and decomposed by the acid. In specimens of *Heliopora* which have been slowly decalcified in chromic acid, the appearance presented by one of these growing points as viewed from below is shown in Plate 8. fig. 6. Here it will be seen that a mass of tissue composed of extremely fine fibre (B) occupies the space immediately within the layer of connective-tissue cells. The fibres composing the mass are disposed in a concentric manner externally around the centre of the mass, and more internally around two rounded cavities situate side by side in its centre. Appearances similar to this are presented by a section of *Heliopora*, prepared as described, cut parallel to the surface and viewed from beneath, sometimes two and sometimes one cavity appearing in the fibrous mass. The fibrous masses occupy the position which in the undecalcified coral is occupied by the projecting points of the corallum, and are identical in structure with the small investment of fine fibrous tissue which can be obtained from a growing point of the corallum by decalcification. But the quantity thus derived from a portion of the corallum cleaned with potash is very small, and bears no proportion to the mass shown in fig. 6. The spaces A, B were probably occupied by the central parts of two newly formed excrescences on a projecting point of the corallum, whilst the hard tissue was extended thence for some distance amongst the fibrous tissue, but how far is uncertain. I have not been able to prepare sections of hard and soft parts in contact which will show this.

I have not seen the finely fibrous tissue in the deeper parts of the corallum; but in some preparations it is to be recognized in longitudinal sections, as at Plate 9. fig. 10, P, though here not showing the fibrous structure.

It seems probable that the layer of connective-tissue cells produces the finely fibrous tissues, and that within this tissue the calcareous matter is deposited from within outwards, the fibrous tissue gradually being removed and absorbed. The finely fibrous tissue may be termed calciferous. Exactly similar tissue with similar concentric fibrillation occurs in similar relations in *Pocillopora*, though here the connective-tissue cells are perhaps absent.

In no part of the growing points of the corallum of *Heliopora* is there any trace of the calcareous tissue being built up of the fusion together of a network of spicules, as

is the case in the corallum of *Corallium rubrum* and also in *Tubipora*, as may be seen at once by examining the growing end of the tube of a spirit specimen of *Tubipora**. In this respect *Heliopora* differs most markedly from both *Corallium* and *Tubipora*. The structure of the hard tissue of *Heliopora* is, however, in many respects very like that of the sclerites of *Primnoa*.

Blue Coloration of the Corallum.

The corallum of *Heliopora* is coloured of a deep blue, and has always been regarded as remarkable amongst corals for this fact. Now that it is known to be an Alcyonarian structure the fact is less exceptional, since both *Corallium* and *Tubipora* have a deeply coloured corallum, and many other Alcyonarians have coloured spicules. Amongst Hexactinians *Stylaster*† *rosaceus* is of an intense red, and the corallum of some Fungias is also red; also that of certain Eupsammidæ, but amongst these the condition is exceptional.

The blue tint is seen in sections of the corallum to be diffused within the hard tissue. The colour is faint or almost absent in the freshly growing tips of the corallum, and pale in the most recently formed superficial structures generally; it is darkest in the layer beneath these in the recently matured tissue. In transverse sections it is seen to be darkest at the surfaces of the walls of the tubes and calicles. In vertical sections of the corallum the continuation of the dark blue line marking the margin of the wall of each tube enables the line of the tube to be traced past the superadded tabula, and marks the boundary between the two structures. Very exceptionally, intensely blue streaks are developed more internally on either side of the central canal, as in Plate 9. fig. 12, where B marks such a blue band. The usual distribution of the colouring is that shown in Plate 8. fig. 4, where the dark zone at the margin of each tube seen in section represents intense colouring. The tabulæ are almost colourless.

When the corallum is boiled for a long period in caustic potash the blue colour remains unaltered. When the calcareous matter is removed from the corallum by means of hydrochloric acid, the colouring-matter is set free, and remaining suspended in the fluid gives it a blue tint. It is, however, not in solution, but can be observed under the microscope to exist in the fluid in the form of small, amorphous, intensely blue masses adhering to small shreds of tissue, &c., and in this condition may be proved to be insoluble in strong hydrochloric acid. If the coloured solution formed by hydrochloric acid be filtered, the blue colouring-matter remains on the filter, and the filtrate has only a very slight greenish tint.

* This fact concerning *Tubipora* seems not to be well known. Claus, *l. c.* p. 204, says: "Unter Ausschluss von Kalkkörpern entstehen endlich die festen Kalkskelete der Tubiporen und sämmtlicher Madreporarien." The fact was well known, however, to Professor Wyville Thomson, who directed my attention to it. Prof. Thomson does not know, however, where the fact is published (he thinks possibly by Prof. Percival Wright in the 'Ann. and Mag. of Nat. Hist.'). Disks of soft tissue spread from the mouths of the tubes of growing parts of the coral. The disks contain an open network of calcareous matter, evidently composed of fused spicules. The disks fuse with neighbouring ones and form the horizontal laminæ.

† Since the above was written I have proved the Stylasteridæ to be Hydroids.—*July* 8, 1876.

The colouring-matter is dissolved at once off the filter by alcohol, and an intensely blue solution, very like that of sulphate of copper in colour, is thus obtained. The colour, however, is not dissolved out of the corallum by the action of alcohol alone. The deep blue and alcoholic solution gives a spectrum in which all the violet, red, and yellow are totally absorbed, and the green and blue alone transmitted. The absorption of the violet end of the spectrum extends to G, that of the less-refrangible end to a little short of E. Addition of potash or ammonia solutions to the blue solution changes the colour to a dirty green, which is contained in a flocculent precipitate. The blue colour reappears on the solution being rendered again acid.

In Bronn's 'Klassen und Ordnungen,' 1860, "Actinozoa," p. 22, is an account of the analysis made by the younger Silliman, at the request of Dana, of various coralla. Amongst the species analyzed was *Heliopora*. Mr. Silliman therefore probably investigated the colouring-matter of this coral at the time when he submitted it to analysis.

On the Structure of the Soft Tissues of Heliopora.

The arrangement of the structures constituting the general superficial layers of *Heliopora*, and of those common to the cœnenchymal tubes and calicles, will be considered in the first place, and in the second the structure of the polyps themselves.

As in other Alcyonarians the various structures are to be classed as belonging to an ectoderm, mesoderm, and entoderm. The general arrangement of these three layers of tissue will be seen in Plate 8. fig. 1.

The *ectoderm* consists of a layer of epithelial cells, which invests the whole external surface of the coral with a uniform covering. Its structure is shown in Plate 9. fig. 10. The cells composing it are elongate and club-shaped, with wide rounded summits and pointed lower extremities, which run out into fine threads which can be traced some way into the layer beneath them. The cells contain a nucleus and nucleolus, and their general contents are finely granular; they are closely packed side by side, placed parallel to one another, and vertically to the surface of the coral. When the epithelial layer is viewed from above, the ends of the cells present a series of polygonal areas. The cells are about ·02 millim. in length. Between the contracted bases of these cells are other irregularly shaped cells with similar nuclei and contents, and also scattered throughout the layer are to be found nematocysts. The ectoderm is prolonged to form the lining of the stomachs of the polyp; otherwise it is superficial only.

The *mesoderm* consists of three different histological structures:—(1) A nearly homogeneous transparent connective-tissue; (2) layers of connective-tissue cells; and (3) masses of finely fibrillar tissue.

(1) Beneath the ectoderm is a thick layer, of a mean thickness of about ·07 millim., likewise extending over the whole surface of the coral, which consists of a highly transparent connective-tissue, which is almost homogeneous, but in which faint lines indicating slight fibrillation may here and there be seen.

Extensions of this homogeneous layer form the central layers of the membranes

lining the cœnenchymal tubes and calicles, and the median plates of the mesenteries, part of the wall of the stomach, &c. The layer immediately beneath the ectoderm is pierced by the superficial system of canals and traversed by the projecting points of the corallum, Plate 9. fig. 10. Nematocysts occur in this last-mentioned layer. They are extremely small, measuring only ·009 millim. in their longest diameter. They are of an ovoid form, and contain a single filament within wound in a spiral whose axis corresponds to the long axis of the cell. They are often to be seen with the thread emitted and twisted in a loop against the side of the cell, which frequently assumes after the ejection of the thread a reniform outline, Plate 9. figs. 13, *b*, *b'*. They are so small that they might readily be overlooked, and a very high power is required to determine their structure. They appear to be not very abundant. They are seen *in situ*, Plate 9. fig. 10, N.

(2) Imbedded within the superficial homogeneous layer of the mesoderm occur also fusiform and branched connective-tissue cells, which are associated together in elongate, often nearly linear groups, Plate 9. fig. 10. Many of these cells are branched, throwing off fine filamentous processes in various directions. Layers of similar cells lie everywhere next opposed to the hard tissues of the living corallum, as has already been described. These cells do not compose any portion of the polyps themselves, but merely line the calcareous calicles.

(3) In decalcified preparations of *Heliopora* enclosed within the layers of connective-tissue cells, at the places before occupied by the growing points of the corallum, occur the masses of very finely fibrillar calciferous tissue already described, Plate 9. fig. 10, P. Both this and the corallum itself belong to the mesoderm.

The *entoderm* consists of spherical cells, each with small transparent nucleus and contents, consisting of irregular yellow pigmented masses and dark coarse granules. They have a mean diameter of about ·014 millim., but vary much in size. They are most probably ciliated in the fresh condition, as are the closely similar entodermic cells of other Alcyonarians. I have not been able to see cilia in the hardened specimen which I have examined; nor have I in these specimens been able to detect differences between the entodermic cells lining the cavities of the calicles and tubes and those lining the canals. Some of the cells show a division of their contents into four (Plate 9. fig. 13, *a*, *a'*). The entodermic cells form layers lining the canals, the cœnenchymal tube-cavities, the cavities of the calicles, and interseptal spaces.

The cœnenchymal tubes in their upper cavities are thus lined throughout by a membrane consisting of three layers, viz. an outer layer of connective-tissue cells, a middle layer of homogeneous connective-tissue, and an inner lining layer of entodermic cells. The calicles are lined throughout in like manner. The arrangement will be seen in Plate 8. fig. 4. In the membrane lining the calicles, in transverse sections a peculiar structure (shown Plate 8. fig. 3) is to be constantly observed. Stout offsets from the median connective-tissue layer pierce the outer layer of connective-tissue cells, and hang loose externally as flattened tags, which appear as if broken off, and are

often somewhat curled up. I have been unable to determine the connexion of these tags of tissue with the calicular wall, Plate 8. fig. 3*. Beneath the uppermost tabulæ scarcely any organic lining remains to the tubes, if any at all, and the deeper central parts of the corallum are, in the specimen of *Heliopora* which I have examined, almost entirely filled with the tubes of the boring annelids (*Leucodora*, sp.). Thus when a mass of *Heliopora*, after being hardened, is decalcified, the whole of the deeper parts are removed, and a thin layer of soft tissue only remains behind, which above presents a similar appearance to that of the surface of the undecalcified coral, but beneath is seen to be composed of a series of villi with the bottoms of the calicular sacs appearing as tubercles amongst them. Since the tubes of the cœnenchym and calicles have no lateral connexions with one another except close to the surface of the corallum, in decalcified preparations they are, excepting at their very upper extremities, entirely separated from one another; hence it is extremely difficult to prepare fine transverse sections in the deeper regions, since the structures afford no support to one another.

Canal-systems.—The summits of the cavities of the sacs of soft tissue lining the cœnenchymal tubes communicate freely with one another and with the cavities of the polyps by means of a system of short transverse canals, which cross over the margins of the walls of the calcareous tubes at the lower parts of their mouths, as already described, p. 97, and shown, Plate 9. fig. 7. The tubes are mostly very short; they are circular in section, and have the same three layers in their walls as have the sacs within the tubes. In older parts of the coral, where the calcareous tubercles on the surface are much developed and the mouths of the cœnenchymal tubes contracted, a series of open channels appear in the corallum at the bases of the superficial papilliform eminences, when the coral is looked at with a hand-magnifier. It is in these channels that the system of transverse canals runs. This canal-system I have termed the "deep canal-system," to distinguish it from the system of smaller canals lying superficially to it. The tube-cavities communicate with the polyp-cavities by means of the transverse canal-system, through a system of large apertures shown in Plate 9. fig. 8. These apertures open in the intermesenterial spaces all around the summit of the calicle, a single one being situate in the space formed by each externally projecting fold of the calicular wall.

The superficial canal-system consists of a series of small canals and sinus, which take mostly a more or less vertical direction, and communicate directly with the deep canal-system. These superficial canals anastomose with one another by horizontal offsets. A series of horizontally extended canals of this system surrounds each contracted polyp, the canals taking a radial arrangement. One such canal is shown in vertical section in Plate 9. fig. 7, and the appearance of the summits of the canals as seen from the surface of the coral is shown in Plate 8. fig. 5. The superficial canals are not only lined by, but also always more or less filled with entodermic cells.

* Exactly similar structures occur in *Tubipora*, being specially developed around the lower part of the polyps.

Openings to the exterior other than those of the polyps were carefully sought for over the surface of *Heliopora*, but without success. The spots from which, by decalcification, growing tips of corallum have been removed, often form themselves into apertures in horizontal sections, and are apt to mislead the observer.

Structure of the Polyps of Heliopora.

The polyps of *Heliopora* have been examined by me only in a contracted condition.

When the contracted polyps are viewed from the interior they show (Plate 8. fig. 5) eight symmetrically and radially disposed lobes, separated by deep sulci corresponding to the insertions of the eight mesenteries into what would be, in the expanded condition of the animal, part of the lateral wall of the polyp. The lobes show a distinct striation in the direction of their length, indicating probably the presence of fine muscular fibres in their substance. At their inner region the lobes show, near their common centre, a number of extremely small nuclei upon their surface. The lobes just described form a covering closing the mouth of the calicle.

From the centre of the disk of lobes a tubular cavity, which may be called the atrium, leads down directly to the mouth (Plate 8. fig. 1); and around the mouth and just above it orifices of the eight tubular introverted tentacles open into the atrium. The tentacles in the retracted condition are completely introverted and appear as tubes, the inner cavities of which would, in the expanded condition of the polyp, form the outer surface of the tentacle. The cavities of the introverted tentacles communicate directly with the atrium, as may be seen in vertical sections, by orifices which show in the centre a cruciform lumen (Plate 8. fig. 1, T') formed by the folds of the ectodermic lining of the tentacular cavity. The retracted tentacles are directed at first horizontally outward from the atrium, and then turned downwards at nearly right angles to their former course. The tentacles rest in the intermesenterial spaces. Transverse sections of four of them are seen in Plate 8. fig. 3. The cavities of the introverted tentacles are lined by a direct continuation of the ectoderm, which passes down over the inner surface of the atrium to enter these cavities. In their interior it is elevated into a series of short stout tubercles, which no doubt project much more in the expanded condition of the tentacle, rendering it compound as in other Alcyonarians. In the tentacles, as seen in Plate 8. fig. 3, three layers, outer entodermic, median connective-tissue, and inner ectodermic, can be readily distinguished. The median probably contains muscular structures, but I have been unable to see them.

The stomach of *Heliopora* is closely similar to that of other Alcyonarians. As seen in the contracted condition its walls are horizontally plicate. In transverse sections, as Plate 8. fig. 3, the layers composing its walls are well seen. There is the usual covering of the entoderm; but in the mesoderm, within the layer of homogeneous connective-tissue, a second narrow zone (B, fig. 8) can be detected, which is probably muscular. The inner ectodermic lining is continuous with that of the tentacles, but ciliate. Eight mesenteries completely divide the upper part of the cavity of the polyp

into eight radially disposed chambers. The mesenteries consist of a median plate of homogeneous connective-tissue, which is directly continuous with the similar layer of the lining membrane of the calicular cavity, and also with that surrounding the stomach, and of an investment of entodermic cells covering the median plate on both sides, excepting where the retractor muscles intervene between the two. These retractor muscles form the lower borders of the mesenteries; they consist of long stout fibres which, lying on the surface of the mesenteries, take origin from the lower part of the sides of the polyp-cavity, reaching down sometimes as far as the margin of the tabula, and curve inwards and upwards, becoming gradually more concentrated as they ascend to be inserted round the mouth and region just below it, in the intervals between the bases of the tentacles.

The muscles have in position, with regard to the plates of the mesenteries, the same arrangement which Kölliker has described as existing in the Pennatulidæ, and which has also been found in the genus *Umbellula* by Lindahl and figured ("Om Pennatulidslägtet *Umbellula*," till Kongl. Vet. Akad. inlemnad den 10. Feb. 1874: Stockholm, tab. 1. fig. 8)*.

The arrangement of the muscles is seen in Plate 8. fig. 3, where R M, R M are the muscles. At opposite ends of the long axis of the stomach the muscles are on opposite sides of the mesenterial plates. The mesenterial chamber (seen beneath in the drawing), which is free of muscles, is the "Dorsalfach" of Kölliker; the opposite one the "Ventralfach." The muscles are covered by the entodermic layer, and are in direct contact with the median plates of the mesenteries, being modifications of the mesoderm.

I have not been able to find any definite protractor muscles in *Heliopora*. I have, however, occasionally seen fibres on the surface of the mesenteries at the lateral margins of the atrium, coming apparently from the stomach-wall, which may prove to be such. In transverse sections I have seen no trace of such muscles.

Heliopora having commonly twelve so-called septa and eight mesenteries, a definite and regular relation of the eight septa to the twelve plications of the wall of the calicle might naturally be looked for; none such, however, exists. As has been before stated, the number twelve is by no means constant; and where twelve are present the arrangement varies in all kinds of ways. In Plate 8. fig. 3 the plications are shown in a section, and their relations are accurately copied. Here there may be counted either twelve or thirteen such plications, representing corresponding calcareous septa in the indentations.

There are eight mesenterial filaments, as usual, present, which spring from the angle where the retractor muscles are inserted into the stomach-wall, and are continued down the free borders of the muscles, being attached to them. The filaments have the usual structure. Two filaments appear to be constantly longer than the others;

* Professor Schneider and M. Röttekken must certainly have been mistaken in their conclusions concerning the arrangement of the muscles with regard to the mesenteries in Alcyonaria, if the figure given in the 'Ann. & Mag. Nat. Hist.' 1871, vii. p. 437, as representing them be correct.

but I am uncertain about this point, it being very difficult to get a view of all the filaments uninjured in any one polyp. To which sides of the mesenterial plates the filaments are attached I have not made out.

Out of at least a hundred polyps examined from the colony of *Heliopora* hardened for examination, only three were found to contain generative organs; in each of the cases ova. In two of the polyps a single ovum only was present, in the third four ova attached singly to four mesenteries. The ova are attached to the edges of the muscular margins of the mesenteries at a point about halfway between the origin and insertion of the fibres composing the lower border of the muscle (Plate 8. fig. 1). The ovum is attached to this border by a specially developed mass of entodermic cells, and at its point of attachment is in close relation with the mesenterial filament. The ova, as shown (Plate 9. fig. 14), are large, measuring ·21 millim. in diameter (the smallest observed measured ·17 millim. in diameter); they are composed of an outer membranous capsule, by means of which they are attached in position, containing a mass of yelk-globules, in which lies a germinal vesicle and germinal spot.

It was not determined which of the mesenteries bore ova, or whether those with long filaments bore them or not, the expectation that abundance of fertile polyps would be found for examination having been disappointed. In Plate 8. fig. 1 the mesenterial filament is, in the drawing, stopped short above the ovum in order to allow it to be seen. The filaments belonging to the septa bearing ova hang down below the ova. No trace of any male elements was found in any polyp. The colonies of *Heliopora* are probably unisexual.

The investigation of the positions of the dorsal and ventral aspects of the polyps in the *Heliopora* colony relatively to the axes of growth is extremely difficult, because when a horizontal section is cut sufficiently deep down to display the muscular arrangement, nothing remains to hold the various sections of polyps in position but the imbedding substance made use of; and where the only substance at command, as in the present case, is wax, the sections with the wax unremoved are almost too opaque and indistinct for observation. By examining such sections, held together by the wax and made transparent with glycerine, I have found that the polyps (although they are often turned on their central axes to a considerable extent, so that the long axes of their stomachs are not by any means parallel, but often inclined to one another at very considerable angles) have nevertheless their dorsal surfaces or the intermesenterial spaces devoid of retractor muscles ("Dorsalfächer") always nearer to the summits of the colony than are the "Ventralfächer." The "Dorsalfächer" thus show a general tendency to take a superior position, *i. e.* lie uppermost, in the vertical plates of which the colony is composed. The entire coral makes up a flat plate, with two outer surfaces, towards which the polyp-tubes are directed in curves on either hand from the vertical axis of growth; and the polyps thus curving away from one another have their "Dorsalfächer" approximated or are placed back to back.

On the Structure of Sarcophyton, *sp.*

An Alcyonarian dredged in shallow water amongst the reefs on the shores of the Admiralty Islands was examined in order to compare its structures with those of *Heliopora*. The Alcyonarian in question appears to belong to the genus *Sarcophyton* (Lesson) M.-Edwards and Haime ('Hist. Nat. des Coralliaires,' t. i. p. 122), originally described in the 'Zoologie du Voyage de la Coquille,' Zooph. p. 92 (1831). The genus is stated by M.-Edwards to be imperfectly known. The specimens correspond in every particular with the description as given by M.-Edwards. The Alcyonarian has exactly the form of a mushroom, with a cylindrical stem and polyps confined to the upper surface of the pileus. Many specimens were obtained, but unfortunately only one retained for dissection, the remainder being packed away.

In this specimen the pileus is about 5 centims. in diameter, being somewhat oval in outline; the height from the bottom of the stem to the summit of the pileus is also about 5 centims.; the diameter is about 1·5 centim. The colony is of a uniform brown colour.

By Claus (*l. c.* p. 208) a genus of the Alcyoninæ, called also *Sarcophyton*, is given as founded by Sars. I do not know whether the old genus *Sarcophyton* has been abandoned and the name used again, or whether there is some error here. The form now under consideration certainly belongs to Lesson's genus, and possibly to the species *lobatum*. On examination the *Sarcophyton* was found to present many points of interest, especially in comparison with *Heliopora*; a short description of its anatomy will therefore be given.

As in Pennatulids two kinds of individuals, sexual and asexual, polyps and zooids, compose the *Sarcophyton* colony. The stem of *Sarcophyton* consists of a series of tubular canals running parallel to one another vertically, and bound together by abundant transparent connective-tissue, in which are closely packed, numerous, stout, calcareous spicules of the common elongate cylindrical form, pointed at both ends, and covered with small lateral tubercles. The canals are prolongations of the polyp-cavities from above. The surface of the stem and under surface of the pileus are covered with an even coat of epidermis, and entirely free from polyps or zooids. On the upper aspect of the pileus the surface is covered all over with polyps or zooids. Over the general upper surface the polyps are pretty evenly distributed at intervals, the interspaces being filled by numerous zooids; but at the margin of the pileus, where its edge is turned down and slightly recurved, is a narrow zone all round, occupied by thickly set polyps with very few zooids. In a vertical section through the central axis of the whole colony, the polyp-tubes are seen to be arranged with great regularity, converging in curved or vertical lines, according to position, towards the stem. The circular areas occupied by the retracted polyps measure 1·4 millim. in diameter, those occupied by the zooids ·42 millim. in diameter—the difference in dimensions being here much less than in deeper regions of the colony, where the polyp-cavities widen

and the zooid-cavities contract. There are narrow intervals between the circular areas, in which there project the thickly set tips of spicules showing through the epidermis (Plate 9. fig. 9) and forming stiff supports to the walls of the cavities.

The structure and relations of the zooids and polyps are seen in Plate 8. fig. 1. The polyps present no remarkable features; they have numerous fine spicules in their antennæ, which are, as is usual, simply retracted, and are provided with protractor and retractor muscles. Of the protractor muscles (P M in fig. 2) part of the fibres appear to be inserted into the wall of the polyp-cavity, whilst others are continued on the inner borders of the mesenteries.

The muscles are arranged with regard to the septa as in *Heliopora*, Pennatulids, and *Umbellula*, showing a dorsal and ventral intermesenterial space; and here the protractor muscles were seen to be placed on the opposite sides of the mesenterial plates to the retractors. Two mesenterial filaments are longer than the rest; probably they are those of the "Dorsalfach," since the only two retained by the zooids are the dorsal ones. The ova are developed deep down in the polyp-cavities; they have the usual form of the ova of Alcyonarians. They measure, when mature, about 7 millims. in diameter. They are placed in Plate 8. fig. 2 at a greater height up in the cavity of the polyp than that at which they usually occur. Ova are to be found in the tubular prolongations of the polyp-cavities very deep in the colony.

The polyp-cavities widen out beneath the surface to contain the polyps and gradually contract again below; they have an extreme diameter of about 2 millims. against a diameter of about ·35 millim., which is that of the tubular cavities of the zooids. The zooid-cavities are only about one fifth the length of the polyp-cavities. The zooid-cavities contract below, and their tubes gradually narrowing join the canal-system, as is described by Kölliker to be the case in *Sarcophyllum* (Kölliker, *l. c.* 1^te^ Abth. Taf. viii. fig. 68). The zooids (Plate 9. fig. 9) consist of a simple globular stomach lined within by a thick epithelium, a prolongation of the ectoderm, and communicating with the exterior by a narrow tubular mouth; they have no trace of tentacles. The inner surface of the stomach is covered with long cilia, directed downwards and inwards. Near the surface of the body, just beneath the ectoderm, eight mesenteries are present in all the zooids; but four of these extend to a much less depth than the others, and hence in a horizontal section at a very slight depth from the surface all the zooids in section are seen with only four mesenteries. The four deeper mesenteries are those attached to the ends of the long axes of the stomach, *i. e.* the dorsal and ventral. Only two mesenterial filaments are developed in the zooids, and these are those of the dorsal mesenteries. The filaments are attached throughout their length to the margins of the septa. The zooids are without sexual organs. The body is covered with an ectoderm resembling in structure that of *Heliopora*; but it was not sufficiently well preserved in the available specimen to show its exact structure. No thread-cells were found in the *Sarcophyton*. The mesoderm forms a sarcosome consisting of tongh, gelatinous, transparent connective-tissue, in which are distributed,

somewhat sparsely, very small finely ramified nucleate corpuscles. In the walls of the zooid- and polyp-cavities there is to be seen a transverse fibrillation of a part of their mesodermic layer; and the wall, when seen in section on edge, shows a layer next the cavity of the polyp or zooid consisting of true transversely directed fibres.

The sclerites or spicules are imbedded in the thick layers of the sarcosome intervening between the zooid- and polyp-cavities and between the tubes composing the stem, besides being found in the tentacles. The growing tips of the spicules project up amongst the ectodermic cells (Plate 9. fig. 8), carrying with them their investment of connective-tissue. When the spicules are removed by acid, corresponding cavities are left in the mesoderm. A transparent membrane can be distinctly seen investing closely each spicule; no structure, however, could be seen in the membrane. The polyp- and zooid-cavities, and the whole of the canal-system, is invested as usual by an entodermic layer, consisting of spherical cells with yellow contents exactly like those of *Heliopora*. In the zooid-cavities, at their summits, around the top of the stomach, masses of these cells were always observed to be accumulated. Possibly the accumulation of these in this situation is consequent on action taking place on the death and contraction of the colony when placed in spirits.

Sarcophyton is an extremely favourable subject for the examination of the vascular system. In sections from alcoholic specimens preserved in glycerine jelly the whole ramifications of the vessels are most clearly displayed. Owing to the pigmentation of their lining entoderm, the canals show out dark and defined in the perfectly transparent connective-tissue. The arrangement of the canals is shown in Plate 8. fig. 2.

Two systems of canals are to be distinguished—the transverse and vertical systems. The transverse canals run parallel to the surface of the colony and to one another in each interspace between the polyp-cavities. They take the most direct courses to connect the cavities of the polyps with those of the surrounding zooids and with those of the adjacent polyps. They commence to be given off laterally from the polyp-cavities at their very summits, forming there communications with the zooid-cavities. They continue to be given off at tolerably regular intervals, crossing now to a closely situate zooid, now to a distant one. Deeper down in the colony the canals make long stretches to join the next adjacent polyp-cavity, and become shorter and shorter as the polyp-cavities converge below. Similar short canals connect the zooid-cavities with one another. Running in a general vertical direction between these transverse canals are the vertical canals, distinguished by their more undulatory course. The chief stems of this system of canals are the direct prolongations of the zooid-cavities. In connexion with these canals is an irregular meshwork, by which the whole deep connective-tissue is permeated, and through the meshes of which the transverse canals pass. Offsets of the vertical canal-system pass between the zooid-cavities, and between the polyp-cavities and zooid-cavities give off transverse connecting branches.

There is no surface network of canals present in the superficial layer of mesoderm directly beneath the ectoderm as there is in *Heliopora*.

The large canals in the stem of *Sarcophyton*, which are in reality long drawn-out prolongations of the body-cavities of the polyps, may be considered to correspond to KÖLLIKER's "sinus;" the vertical and transverse canal-systems to the "canales nutrici majores;" the network in connexion more directly with the vertical system to the "vasa nutrica minora." Apparently there are no vessels corresponding to the "vasa capillaria," their place being occupied by the network formed by the small ramified corpuscles in the sarcosome.

The transverse and vertical canal-systems anastomose with one another frequently, but only here and there. Occasionally, but rarely, the canals from the bottoms of the zooid-cavities join directly the transverse canals. The canals have a wall of fibrous tissue directly continuous with the fibrous layers of the zooid- and polyp-cavities, and are lined internally by entodermic cells, Plate 9. fig. 9, C. Sac-like enlargements or swellings are constantly to be seen on the canals of *Sarcophyton*, both near the surface and in the deep tissue. In one such swelling was found a parasitical cyst of oval form and with greenish contents; its nature could not be determined. The polyps in *Sarcophyton* are so disposed that they have the dorsal intermesenterial spaces directed towards the centre of the pileus, and at the verge of the pileus these spaces uppermost. At least this disposition was observed to hold good in three opposed radial directions from the centre of the pileus. A whole specimen was not available for examination.

As in *Heliopora* the polyps are not disposed with perfect regularity in this manner, so that radial lines from the centre of the pileus would pass directly through their longer diameters. Many of them are rotated more or less on their axes, so as to be inclined to the radial lines. They are most regular in disposition at the margin of the pileus. The zooids, though preserving a general uniformity of arrangement, which proves their single pair of mesenterial filaments to be the dorsal ones, are still more irregular in disposition.

Notes on the Structure of two Species of Millepora.

I have examined the structure of two species of *Millepora*; one, *Millepora alcicornis*, was obtained at Bermuda, the other species was found at Zamboangan, Mindanao, Philippine Islands. The investigation of the structure of the genus *Millepora* is beset with unusual difficulties. The calcareous tissue of the coral is very hard and compact, and the soft tissue, on the other hand, very soft and very much altered and shrunk by the action of spirit. Further, the polyps are extremely small. I give here only a few results at which I have arrived from the examination of the material which I have at present at command. I hope to obtain abundance of *Milleporæ* at Hawai and Tahiti, and to make a thorough investigation of their structure.

The corallum of *Millepora*, although in its histological structure it resembles *Heliopora* very closely, being formed of a similar fibro-lamellar tissue, differs extremely from *Heliopora* in the coarse arrangement of its components. Instead of being composed of a series of parallel tubes divided by tabulæ, the corallum of *Millepora* is composed of a net-

work of tortuous branches of hard tissue, with cavities of two kinds, smaller and larger. In *Millepora alcicornis* the calcareous meshwork is comparatively open. In the Philippine species, in which the polyps are extremely minute, the cœnenchymal tissue is much more compact—so much so that instead of, as in *M. alcicornis*, the hard and soft parts appearing to form equally complicated meshworks, the soft tissues appear to occupy a series of tortuous canals bored in the compact cœnenchym; and in finely ground sections these canals becoming filled with *débris*, and thus as it were injected with opaque matter, stand out black in relief when the sections are viewed by transmitted light, and show the relations of the hard to the soft parts in a very clear manner. The tortuous tubes channelled in the hard cœnenchym are seen to lead from the calicles in all directions, and anastomosing freely with one another to join the cavities of surrounding calicles.

When a mass of *Millepora* hardened in alcohol is decalcified, a thin layer, consisting of almost the entire living substance of the coral, separates from the surface, and, as the only residue of the deeper tissues, a greenish gelatinous mass remains. The superficial layer thus separated consists of an irregular network of tortuous canals, which in the recent state occupied the canals in the hard cœnenchym or were interwoven with its equally complex meshwork. The canals are filled with round cells, resembling the endodermic cells of Alcyonarians; their walls are thickly beset with the large thread-cells, which have already been described and figured by Professor Agassiz. The cells are ovoid, and are provided with a long filament armed near the end with a spiral of spines. The thread-cells are developed in special large transparent sacs, and are seen in all stages of formation. Two kinds of thread-cells are present, the larger ones just described, and others of nearly the same form, but of not more than one fifth the length, which small thread-cells are confined to the tentacles, on the surfaces of which they are densely set. The larger thread-cells are especially abundant round each polyp, forming a zone around it. The canals are covered externally with a transparent tissue, probably calciferous in function. In certain places in the *Millepora* obtained at Zamboangan here and there canals larger than the others, chief stems as it were, are to be found running a long straight course on the surface for an inch or more, and giving off branches on either side. Canal offsets of the general meshwork join the polyp masses all around in a radiate manner. The larger polyps, as seen from above, have an irregular indented outline, whilst the smaller are simply circular or nearly so. The larger are less numerous than the small. Tentacular masses covered with the smaller thread-cells can be seen in the apertures of the polyps of both kinds. Their number could not be determined with certainty, since it is impossible to define the exact limits of the contracted lobulate masses and distinguish a mere lobe of a tentacle from an entire tentacle. In the larger polyps, however, there constantly appeared to be four. Professor Agassiz saw and figured four tentacles only in *Millepora alcicornis*. Pourtalès says that the tentacles appeared to him "rather as tentacular masses studded with lasso-cells, five in number." From the appearances which present

themselves in fine vertical sections of the polyps of *Millepora alcicornis*, I think I cannot be mistaken in the conclusion that the tentacles of the polyps are compound, consisting of a broad central portion provided with five or six short pinnæ on either side. Such tentacles might well appear as tentacular masses if not quite fully expanded*. The tentacles are simply retracted. The layer of cells covering their exterior is continuous with that lining the cavity into which they are retracted, and ectodermal in character. In vertical sections in *Millepora alcicornis* the stomachs of the polyps are seen to be cylindrical in form, but drawn out and widened below by the action of retractor muscular fibres which are attached around their bases. The stomach-cavity is lined with very large, inflated, transparent, cylindrical cells. The stomach has externally to this a fibrous or muscular wall, which is again covered externally, as are the tentacles, by a layer of cells reflected from the wall of the cavity in which it is retracted. In transverse sections the stomach has its lining cells sometimes so arranged as to show an exactly cruciform central opening between them, the outline of the stomach being quadrangular, with the points of the cross directed to the angles, in other cases the opening is three-rayed. The retractor muscular fibres attached to the stomach are seen, on viewing the organ in horizontal sections from beneath, to radiate out from its margin all round, and to be attached to the cœnenchymal canals, which, as before described, likewise radiate from the polyp masses. The fibres often pass a considerable distance along the canals before they are lost to view. The radiating muscular fibres, which are fine and transparent, are gathered here and there into bundles, and sometimes appear as if arranged in a regular radiating system. Fibres are present radiating at slightly different depths all round the circle. No trace of radially disposed mesenteries has been detected in *Millepora*, though fine transverse sections have been obtained. No continuous ectodermic layer covering the outer surface of *Millepora* has been found; such must be present, but it has only been observed indistinctly in fragments in *M. alcicornis*, where it is extremely delicate. The specimens of both species of *Millepora* obtained were without generative organs.

The greenish mass left behind as representing the internal structures of the Zamboangan species of *Millepora* after decalcification is extremely delicate and transparent. It was only observed in the *Millepora* obtained at Zamboangan, where its green tint rendered it conspicuous. The green tint on examination of the mass with a high power is found to be caused by a tangle of the filaments of a vegetable organism which bores the hard parts of the coral in all directions, and of a slight transparent residue from the decalcified corallum.

Notes on the Structure of Pocillopora, *sp.*

A species of *Pocillopora*, possibly *P. acuta*, was obtained at Zamboangan. A pre-

* *July* 8, 1876.—Since the above was written I have found that these appearances are due to the presence in the smaller zooids of large numbers of short knobbed tentacles, which become massed together in the retracted condition of the zooid.

liminary examination of its structure gave the following results:—The histological structure of the corallum of *Pocillopora* differs from that of *Heliopora* and *Millepora* in that its hard tissue is composed of definite prisms of calcareous matter, the polygonal ends of which prisms can be seen when the systems in which they are disposed are viewed end on. The prisms further show a transverse banding, appearing something like that of transversely striped muscular tissue. The corallum is excessively hard and compact.

When the coral is decalcified, a very thin continuous membrane separates from the surface with the entire structure of the polyps disposed within it at intervals. The membrane shows little structure, consisting, as it does, of a thin epithelial ectodermic layer and of a layer of connective-tissue. It is devoid of thread-cells and of any canals or vessels. Beneath it shows small masses of concentrically wound fine fibres, where the projecting points of the corallum have rested, just as in *Heliopora*.

The polyps have very shallow cavities, as necessitated by the form of the corallum. They have twelve tentacles, six intermediate ones of which are smaller than the others. They have the usual twelve mesenteries, and have long mesenterial filaments coiled up in the intermesenterial spaces, though how many of these filaments are present is uncertain.

The specimen of *Pocillopora* examined was devoid of generative organs. The deep tissue of *Pocillopora*, when decalcified, yields a delicate gelatinous mass, showing very ill-defined structure, but full of the same vegetable parasite as that which attacks *Millepora*. A further examination of *Pocillopora* will be made at Hawaii.

It has already been stated that Professor Verrill discovered some time ago that *Pocillopora* was a Hexactinian; but I do not know to what extent he carried his examination of the coral.

Note on the Structure of a Stylaster.

Since Kunth, as already stated, has referred to the covering of the mouth of the calicle of *Cryptohelia* as the analogue of the operculum of the Rugosa, I may state that I examined a specimen of a Stylasteracean dredged by the 'Challenger' in 500 fathoms off the Meangis Islands on February 10th, 1875, and with the same result arrived at by Sars in his examination of *Allopora oculina* (Sars, *l. c.*). The Stylasteracean in question is exactly similar in every respect to *Cryptohelia pudica*, excepting that it has no calcareous laminæ in front of the mouth of its calicle.

The tentacles are of a dirty green colour, simple, elongate conical in form, and, as in the case of *Allopora oculina*, they lie *in the grooves between the calcareous septa* and are retracted and protruded in these grooves. The calcareous septa are twenty-two in number, and the tentacles also twenty-two.

The coral when decalcified leaves an organic residue, consisting of an extremely open network of tissue very similar to that of *Millepora*. The network forms a very soft and feeble mass, having the form of the hard parts, the place of which latter is

occupied in part by transparent connective-tissue. From the circle of tentacles a cylindrical cavity, showing twenty-two plications on its wall, leads to the stomach. The stomach is globular, with a long conical mouth or proboscis projecting up in the centre of the last described cavity. A similar proboscis is described by Sars as existing in *Allopora oculina*. The stomach seems to have no outlet below; but it is of course difficult to be certain of the fact in so small and yielding a structure. A series of bundles of fibres, each bundle continuous with one of the plications of the cavity above, is attached to the periphery of the stomach. There are no mesenteries, at least none so distinctly differentiated histologically that they can be recognized by methods which show them plainly in *Heliopora* and *Pocillopora*. Fine transverse sections of polyps stained with carmine were obtained; they showed only the open meshwork of tissue around the stomach, but no definite mesenteries. In the part of the meshwork surrounding the cavity leading from the tentacular circle to the stomach, and just below the level of the tentacles, lie the generative organs. All the individuals of the only stock of *Stylaster* examined were males; hence these corals appear to be dioecious. Very large globular sacs crammed with spermatic cells, containing some of them vesicles of evolution, and others masses of spermatozoa spirally wound, were found in the position above described, attached to parts of the meshwork, and disposed sometimes in a single row around the calyx, sometimes in two rows one above the other. These occupy the interior of the cavities of the ampullæ. No trace of mesenterial filaments was seen in *Stylaster*.

Portions of a *Cryptohelia* examined showed an exactly similar structure to that of the *Stylaster* *. The *Cryptohelia* stock also contained only male generative elements.

Notes on the Parasitic Vegetable Organisms found in Millepora *and* Pocillopora.

The hard tissue of both the *Millepora* and the *Pocillopora* from Zamboangan are traversed in all directions by fine capillary branching canals, bored by some low vegetable organism. The canals are provided at intervals with numerous spherical cavities attached to them laterally, and obviously having contained in the fresh state the spore capsules of the organisms.

The *Pocillopora*, which has an unusually dense and hard corallum, is most thoroughly permeated by three parasites; the Zamboangan *Millepora*, in which the tissue is dense, has them to a somewhat less extent; whilst in the *Millepora alcicornis* from Bermuda, in which the corallum is comparatively soft and cancellar, borings of the parasites can only here and there with difficulty be detected.

The parasites, when set free by acids, are seen to be composed of a ramifying mycelium with abundance of fructification. The parasites are probably similar in nature to those described as infesting the shells of mollusca and other hard animal tissues by Professor Kölliker and Dr. Carpenter, references to whose papers on the subject have already been given. I have seen also a paper on the vegetable parasites in shells

* *July* 12, 1876.—I have since shown that the whole of the Stylasteridæ are true Hydroids.

in the 'Proceedings' of one of the learned societies of Vienna—I think in the 'Sitzungsberichte.'

A remarkable fact is that the parasites are distinctly green, though they appear to be fungi, and those of shells are described as fungi. Possibly the parasites in question have already been described by Professor Kölliker. I have, of course, not access to his paper*.

[Postscript.—Received November 25, 1875.

August 11, 1875, Honolulu.

Since writing as above and since sending off my paper to the Royal Society, I have come upon a passage in the 'Voyage autour du Monde de l'Astrolabe: Zoologie,' Quoy et Gaimard, vol. iv. Zoophytes, pp. 252, 253 (Paris, 1832), which is to the following effect:—

M. de Blainville's observations on the animal of *Heliopora cærulea* led him to remove it from the genus *Pocillopora*, in which it had before been placed, and form the genus *Heliopora* for it, because the *Pocilloporæ* have never more or less than twelve tentacles.

Heliopora has either 15 or 16 short, broad, triangular, pointed tentacles, forming a disk around the mouth. The animals were made out with difficulty with a powerful lens. (Eight compound tentacles have evidently been mistaken for sixteen simple ones.)

Formerly Quoy and Gaimard mistook, on the voyage of the 'Uranie,' the expanded parasitic *Leucodoras* for the polyps of *Heliopora*. They call them small parasitical zoophytes, probably of the class of Annelids.

At p. 245, Quoy and Gaimard describe the twelve short tentacles of *Pocillopora damicornis*. The nature of the polyps of *Pocillopora* was therefore well known long before Prof. Verrill's examination of them†.]

CONCLUSIONS.

Heliopora is most undoubtedly an Alcyonarian. The number of its mesenteries, and the distribution with regard to them of the retractor muscles, the form and number of its tentacles, are decisive evidence in the matter; and this evidence is borne out by almost every item of histological structure. In the peculiar manner in which the retraction of the tentacles takes place, viz. by introversion, *Heliopora* seems to differ from

* Since the above was written I have found the same parasites in various corals from all parts of the world.

† Received February 28, 1876.—In the nurse-stocks of several species of *Fungia* a kind of intracalicinal gemmation appears to take place. On the separation of a young free *Fungia* from the nurse-stock, the next free *Fungia* buds out from the centre of the scar left on the stem, *i. e.* from what has once been the centre of the calicle of the stock. (See Semper, Generationswechsel bei Steinkorallen.) I have lately found a very fine specimen of the nurse-stocks of a large species of *Fungia* at Tahiti, and have been able to see this fact quite plainly. It is owing to this mode of growth that the stems of the nurse-stock become jointed.

all other Alcyonarians except *Corallium**. From both *Corallium* and *Tubipora*, *Heliopora* differs in that the hard tissue of its corallum shows no signs of being composed of fused spicules, but in its histological structure most closely resembles Zoantharian Corals. With the Milleporidæ and with the Pocilloporidæ and Seriatoporidæ *Heliopora* is allied solely on account of its possession of tabulæ. Now that an Alcyonarian is added to the list of various Anthozoa possessing these peculiar structures, their presence becomes of less classificatory importance even than Professor VERRILL proved it to be. There can hardly be a doubt that *Seriatopora* will prove to be, like *Pocillopora*, a Zoantharian; and *Millepora* is certainly very different in structure from *Heliopora*. *Heliopora* thus stands quite alone amongst modern forms; and in the peculiar structure of its cellular cœnenchym it is so remarkable that it is unlikely that on examination of the soft parts of other corals, at present known from their coralla only, any near relatives of it will be discovered. Amongst extinct forms, however, *Heliopora* has several close allies, and the genus itself existed in the Cretaceous period. The genus *Polytremacis* differs apparently only in the more perfect development of the so-called septa, which reach to the centres of the tabulæ. The genus occurs in the Chalk, Greensand, and in Eocene formations. *Heliopora* has, further, a very closely allied palæozoic representative in *Heliolites*, in which the cœnenchymal tubes are provided with very closely placed tabulæ.

The three genera *Heliopora*, *Polytremacis*, and *Heliolites* differ from one another in so slight a degree that they are placed under the one genus *Heliopora* by QUENSTEDT. To include these three genera, a new family of Alcyonarians must be formed, for which the term Helioporidæ appears most suitable, which family may from the recent species be thus characterized:—

Family HELIOPORIDÆ.

A compact corallum present, composed of a fibro-crystalline calcareous tissue as in Madreporaria. Corallum consisting of an abundant tubular cœnenchym, and with calicles having an irregular number of lateral ridges resembling septa. Calicles and cœnenchymal tubes closed below by a succession of transverse partitions. Polyps completely retractile, with tentacles when in retraction introverted. Mouths of the sacs lining the cœnenchymal tubes closed with a layer of soft tissue, but communicating with one another and with the calicular cavities by a system of transverse canals.

The structure of the cœnenchym of the Helioporidæ is entirely unique amongst Anthozoa; no other form has a cœnenchym composed thus of a series of long tubes packed side by side, and lying parallel to the calicular tubes and at right angles to the surface. It is to be remarked that the tubes are like the calicles in being open above,

* I have found no information on this point in any of the text-books; but in SCHMARDA's 'Zoologie' there is a figure of *Corallium*, copied from LACAZE-DUTHIERS's 'Hist. Nat. du Corail,' in which the tentacles are drawn introverted as they are in *Heliopora*.

that they have walls composed in exactly the same manner as those of the calicles, and that they are closed below at intervals in the same way by exactly similar tabulæ. Further, the soft tissues lining the cavities of the cœnenchymal tubes are identical in structure with those lining the calicular cavities, and the same transverse system of canals connects the summits of the tubes with one another and with the summits of the calicular cavities.

It seems by no means improbable that the cœnenchym here is composed of the tubes of absorbed polyps or zooids which have lost the rudimentary organs, which they still possess in such a form as *Sarcophyton*, and have become mere tubular cavities, whose openings to the exterior even have been obliterated; it seems impossible otherwise to account for the presence of the successions of tabulæ in the cœnenchymal tubes. The foregoing considerations are suggested by the circumstance that a series of fossil corals, grouped by M.-Edwards under the Tabulata, appear most probably to have been Alcyonarians as well as *Heliopora*.

The genus *Chætetes* was considered by Keyserling to have belonged to the Alcyonarians, because of the absence of septa in it, and the mode in which its polyps are grouped; but Milne-Edwards retains it amongst the Zoantharians, because of its close resemblance to the Favositidæ, in which the presence of septa is regarded as conclusive in deciding against Alcyonarian affinity. The presence of calcareous septa, however, must now be considered a character of less importance than it formerly was. As is seen in the case of *Heliopora* pseudo-septa may exist, which do not necessarily correspond in any way, in disposition or number, with the membranous mesenteries. In *Stylaster* and *Cryptohelia* the calcareous septa are obviously formed as infoldings of the margin of the calicles. Here the septa are between, instead of opposite to the tentacles; and membranous mesenteries appear to be absent, or at all events rudimentary only. In the Favositidæ the septa seem to have been no more perfect than they are in *Heliopora*, and to have been most variable in number, but often twelve, as also in *Heliopora*. M.-Edwards describes from 10 to 12 septa in *Favosites gothlandica*. In *Michelinia favosa* 30 to 40 subequal septal striæ are to be made out at the upper margin of the wall of the calicle. I cannot refer to specimens; but it seems not unlikely that the septa in the Favositidæ were pseudo-septa as in *Heliopora*, and that these coralla were formed by Alcyonarians, the perforations in the walls having transmitted transverse canals like those of *Heliopora* and *Sarcophyton*, and the coralla being free of tabular cœnenchym, because none of the polyps were aborted as in *Heliopora*. Some Favositidæ seem to have formed a compound colony, consisting of polyps and zooids, as *Favosites Forbesii*, where a few large cells are seen set amongst numerous surrounding small ones. *Heliolites* seems to a certain extent to form a transition stage between a condition such as that in *Favosites Forbesii* and the condition in *Heliopora*; for in *Heliolites*, the more ancient form, the cœnenchymal tubes are regularly hexagonal, and apparently much more nearly equal in breadth to the calicles than in *Heliopora*. In the growing points of *Heliopora* the hard parts are made up of a series of open, often hexagonal tubes, and resemble *Favosites* in their surface aspect. In *Heliopora* the transverse canals pass over

notches in the summits of the walls of the cœnenchymal tubes and calicles, in order to place these cavities in communication with one another. In *Favosites* the calcareous tissue surrounded the transverse canals, and the perforations in the walls of the calicles were thus produced.

If *Favosites* was an Alcyonarian, *Chætetes* was of course also of that group. The genus *Alveolites* amongst the Favositidæ is peculiar for the possession of three tooth-like prominences as the only representatives of septa. One tooth, well developed, is situate inside the calicle; on that side of each calicle which lies externally in the colony, and opposed to this on the tip of the calicle next the interior of the colony, are a pair of rudimentary teeth. This arrangement reminds us at once of the distinction of dorsal and ventral mesenterial interspaces in Alcyonarians, and the direction of all the "Dorsalfächer" in *Sarcophyton* and *Heliopora* towards the central axis of the colony. In *Alveolites* the two teeth seem to correspond to the "Dorsalfach," and the single one to the "Ventralfach," the two teeth having occupied the space devoid of retractor muscles. Kölliker describes a series of teeth as existing at the margin of the calicle in *Renilla*, which follow a constant law in their relation to the septa. When only one tooth is present it is opposite the "Dorsalfach;" when three, one is opposite the "Dorsalfach," and the two others opposite the lateral "Ventralfach." In *Alveolites* the one tooth is ventral instead of dorsal. In *Syringopora* the septa seem to be very much of the same nature as in *Heliopora*; and in *Heliopora*, as already described, the tabulæ are not merely transverse floors, but the bottoms of cups of hard tissue fitted inside the older tubes and calicles. In *Syringopora* this condition of the tabulæ is much more marked, and the corallum appears as if formed of a series of calicles fitted one within another.

A difficulty appears to arise from the peculiar mode of the development of the calicles by budding in *Heliopora*, the foldings of the walls of the calicles being due, to a considerable extent at least, to the formation of these walls from a circle of cœnenchymal tubes. The septa are, however, not entirely formed in this way. It would of course be of great interest to see whether the primitive calicle, in the developing *Heliopora* colony, forms calcareous septa.

Heliopora having so commonly twelve septa, and in conjunction with these eight mesenteries, it was at first thought that here some key would be found to the elucidation of the question of the relations of the tetrameral corals to the Hexactinians; but no definite arrangement of the eight mesenteries to the twelve septa could be discovered. Ludwig and Pourtalès have concluded that the tetrameral condition in the Rugosa is the result of a modification of an originally hexameral arrangement—that the Rugosa are, in fact, modifications of the Hexactinian type. Kunth, however, using similar methods, has come to an opposite conclusion. Now that it is known that an Alcyonarian exists which constructs a solid calcareous corallum, in histological structure scarcely, if at all, to be distinguished from that of many Madreporaria, and that this Alcyonarian also possesses marked calcareous septa, which septa show, notwithstanding

the octameral arrangement of the mesenteries, a hexameral disposition, in being often twelve in number, it seems that the question of the affinities of the Rugosa may fairly be reopened. The presence of well-marked calcareous septa in *Cryptohelia* and other Stylasteridæ (which septa are equal to the tentacles in number, but nevertheless to be regarded, like those of *Heliopora*, as pseudo-septa) is significant. The marked tetrameral arrangement of the septa in Rugosa, and the presence in many forms of tabulæ, are certainly characters not opposed to the alliance of these corals with the Alcyonarians; and the fact that paired series of opercula occur in certain Rugosa, which are compared by Lindström, their discoverer, to the skeletal structures of certain *Primnoæ*, seems to be evidence in favour of such an alliance of the very strongest kind. In no Madreporaria do paired hard structures, at all resembling those of *Primnoæ* or of *Goniophyllum pyramidale*, occur. The opercular structures in the coralla of *Cryptohelia* and *Lepidopora* can scarcely be regarded as comparable with the opercula of Rugosa. The structures are merely folds of the lip of the calicle, and are continuous with it and immovable, not movable separate articulate structures. Many Rugosa show an arrangement which may well be compared to the distinction of dorsal and ventral regions in Alcyonaria. The most important distinctive character of the Rugosa appears to be the occurrence in them, alone of all Anthozoa, of intracalicinal gemmation*.

With regard to *Sarcophyton*, the fact that compound colonies composed of multitudes of zooids, combined with a lesser number of sexual polyps, occur amongst the Alcyonidæ, as well as amongst the Pennatulidæ, in which they are so well known from Kölliker's great work, appears to be new to science. That in such colonies and in *Heliopora* the "Dorsalfächer" are all turned towards the axis of the colony and directed upwards is also a new fact. The zooids in their structure seem to conform very closely to those of Pennatulids (*Sarcophyllum*, e. g.); but to the list of distinctive differences between the zooids and polyps of Pennatulids given by Kölliker, viz. the absence in the zooids of tentacles, the presence of two mesenterial filaments (the dorsal ones), the absence of generative organs, and the shortening of the hypogastric region to such an extent that it fuses with the anastomosing canal-system—to these marks of distinction must be added, in the case of the zooids of *Sarcophyton*, the fact that four of the mesenteries, the dorsal and ventral pairs, are deeper than the others.

It seems extremely difficult to reconicle the extraordinary succession of the mesenteries in the development of the Zoantharians, discovered by Lacaze-Duthiers, with the facts presented by Alcyonarians. Did the development of the eight mesenteries of Alcyonaria correspond with that of the first eight mesenteries formed in Actiniadæ, the first mesenteries formed would be either the lateral dorsal or lateral ventral; but these are those which are most rudimentary in the zooids of *Sarcophyton*. Moreover the mesenterial filaments of the two lateral pairs of septa are in the development of Actiniadæ the first to appear, and not the dorsal, which are longest in the Alcyonarian polyps and

* An examination of the Cornulariadæ, the only recent solitary Alcyonarians, might very possibly throw light on the question of the affinities of the Rugosa.

most persistent in the zooids. Apparently, however, development in Alcyonarians follows a different course.

In *Halysceptrum*, the development of which has been examined by Kölliker, the eight mesenteries appear from the very first. In *Kalliphobe* (Busch), one of the *Edwardsiæ*, according to Metschnikoff, the larva has, in its earliest stage, eight tentacles and two mesenterial filaments.

The peculiarities presented by the Stylasteridæ have struck many observers. M.-Edwards and Haime placed these corals (Stylasteracea) under the Oculinidæ. Gray, however, established a family (Stylasteridæ) for the genus *Stylaster* alone. Pourtalès, who in his 'Deep-Sea Corals' dwells upon the many peculiarities of the corallum of this family, places under it the genera *Allopora*, *Stylaster*, *Distichopora*, *Cryptohelia* *, *Lepidopora*, and *Errina*. The peculiarities in the structure of the soft parts, and the relations of the tentacles to the septa, described in this paper as occurring in a *Stylaster* and a *Cryptohelia*, and the similar facts observed by Sars in the genus *Allopora*, strengthen the facts brought forward by Pourtalès, with regard to the coralla, in a very potent manner. I hope to make a close study of the structure of *Stylaster*. The apparent absence of mesenteries is most remarkable, and a similar condition appears to occur also in *Millepora*. The number of tentacles and septa in the Stylasteridæ seems hardly to follow the usual hexameral law. In the species of *Stylaster* examined by me there are invariably twenty-two septa and twenty-two tentacles. In *Stylaster erubescens*, Pourtalès describes the septa as being in number from nine to twelve, most frequently eleven. In *Allopora miniata* the septa are from seven to ten, generally eight. *Cryptohelia* has commonly sixteen.

With regard to the affinities of the Milleporidæ, no certain conclusion can be arrived at from the few facts yet ascertained. I hope to obtain specimens at Hawaii in sexually mature condition†.

H.M.S. 'Challenger,' North Pacific.
21st July, 1875.

* Pourtalès has remarked that the genus *Endohelia* of M.-Edwards and Haime appears indistinguishable from the genus *Cryptohelia* of the same authors. *Endohelia* is founded on a Japanese species. The 'Challenger' dredged a coral certainly not generically distinguishable from *Cryptohelia* off the coast of Japan.

† Postscript.—Since the above was written I have been able to refer at Honolulu to Prof. Lacaze-Duthiers's 'Histoire Naturelle du Corail.' I therefore add a few notes.

In *Corallium* the contracted polyp presents externally at the surface eight lobes coloured red. When the polyp is expanded, these lobes form a coloured cup with eight dentations at its margin, which surrounds the lower part of the expanded colourless polyp (see pl. 2 of Prof. Lacaze-Duthiers's work). The eight lobes described as closing the mouth of the calicle in the contracted polyp of *Heliopora* probably occupy a similar position, and have a similar appearance in the expanded condition of the polyp.

In *Corallium* the pinnæ or barbules of the tentacles are all severally introverted (*l. c.* p. 57), as well as the tentacles themselves. In *Heliopora* this appears not to be the case. In the hard tissue of *Corallium* boring vegetable parasites occur, as observed in *Millepora* and *Pocillopora*.

I have further been able to refer to Dana's great work on Corals in the splendid collection of scientific works in the Government Library at Honolulu, and to other works relating to *Heliopora*.

Description of the Plates.

Illustrating the structure of *Heliopora cærulea* and *Sarcophyton*, sp.

All the drawings, with the exception of figs. 16 & 17, Plate 9, are by the author of the paper. Figs. 16 & 17, Plate 9, are by Mr. J. J. Wilde.

PLATE 8.

Fig. 1. Schematic representation of a section vertical to the surface of *Heliopora cærulea*, showing the relations of the hard to the soft parts: the hard parts are coloured dark. In the centre is seen in section a fully developed sexually mature polyp in a retracted condition. The calcareous calicle in which it is contained is closed beneath by the tabula (CT), and the walls of the calicle are continued above into points (P) projecting above the general surface of the coral, the section being supposed to be so carried as to pass through two of the calcareous projections which surround the calicle.

Closely applied to the surfaces of the calcareous tissue, and lining its cavities everywhere, is a layer of spindle-shaped connective-tissue cells, between which and the layer of entodermic cells is an interval occupied by transparent homogeneous connective-tissue.

The layer of epithelium (E) covering the whole surface of the coral is seen to be continuous with that covering the exterior of the tentacles (here, from the introversion of those organs, appearing as their interior), whilst the entodermic layer (EN) covers their interior. The tentacle on the right side of the drawing has its tip passed behind the retractor muscle,

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Dana states (U.S. Expl. Exped. vol. vii. Zoophytes, J. D. Dana, Philad. 1846, p. 539) that the blue colour of *Heliopora* is of animal origin and is lost on immersion of the coral in nitric acid. The colouring-matter was not analyzed by Mr. Silliman.

In the Atlas of the 'Voyage de l'Astrolabe,' Zoophytes, pl. 20. figs. 12, 13, 14, the expanded polyps of *Heliopora cærulea* are figured by MM. Hombron and Jacquinot. In fig. 14 sixteen very short, simple, conical tentacles are shown, in fig. 13 only fifteen tentacles. The figures are evidently very erroneous. The corresponding description I have been unable to refer to, the volume containing it being wanting in the Hawaiian Government copy.

In the Zoology of the 'Voyage de l'Uranie,' Quoy and Gaimard, Paris, 1824, p. 656, is a description of the polyps of *Heliopora* (*Pocillopora*) *cærulea*.

The expanded polyps have radiated tentacles, and are said to entirely hide the corallum when they are in an expanded condition. Experiments proved that the communication between the animals is somewhat imperfect, since a stimulus applied to any part of the colony caused only the polyps in that immediate neighbourhood to retract themselves.

In the plates of the 'Voyage de l'Uranie,' pl. 96. figs. 5, 6, 7, *Heliopora* is figured, showing in fig. 5 the appearance of the coral in the fresh state, but without any representation of the polyps.

notwithstanding the actual continuity of the muscle with the mesentery above, in order to show the position of the ovum (O). At the bottom of the atrium, *i. e.* the central canal leading from the mouth and tentacles to the exterior, and formed by the deep retraction of the animal, are shown the mouths of the tubes formed by the introversion of two tentacles as they appear when looked directly into.

On the right-hand side of the figure three tubular cavities (TC, TC, TC), forming the so-called cœnenchym, are represented, lined by their soft tissues, composed of the same three layers as compose the lining of the calicle. Two of the tubes communicate above, over their lateral wall, by one of the deep canals. On the left-hand side of the figure portions of the plates of hard tissue forming the lateral walls of the tubular cavities are shown (A, A), with their natural upper margin. Two systems of canals are seen in section near the surface of the coral. The most superficial canals (V, V, V) lie almost immediately beneath the external epithelial layer; they are more numerous and much smaller than the deeper canals (V′, V′), which form communications between the adjacent tubular cavities passing over the summits of the lower parts of their walls, as is seen on the right-hand side of the figure. Both sets of canals are lined with entodermic cells.

A A. Portions of the walls of the tubular cavities.
CT. Calcareous tabulæ.
P. Projecting points of calcareous tissue.
E. Epithelial layer of ectoderm.
EN. Entodern.
C. Layer of homogeneous connective-tissue.
D. Layer of connective-tissue cells.
T. Tentacles introverted, seen in longitudinal section.
T′. Tentacles introverted, viewed directly into their mouths.
S. Cavity of stomach.
RM. Retractor muscle.
MF. Mesenterial filament.
TC. Tubular cavities of cœnenchym.
V. Superficial smaller vascular canals.
V′. Deep larger vascular canals.

Fig. 2. Section vertical to the upper surface of *Sarcophyton*, sp., showing three sexual polyps and a number of zooids.

The polyps are represented in the contracted condition; they occupy three large elongate cavities in the general transparent sarcosome. The tentacles here are not introverted simply but retracted. The sarcosome between the polyp-cavities is traversed by an elaborate network of canals belonging to two systems, a transverse one, and a vertical one, which, how-

ever, freely anastomose. The transverse canals lead directly from one polyp-cavity to another, with a course nearly parallel to the surface plane of th *Sarcophyton*, or from the polyp-cavities to the zooid-cavities. The vertical system of canals has a tortuous, branching, freely anastomosing course. The zooid-cavities contract at their lower extremities, and pass directly into this system of canals. Prolongations of the vertical system of canals pass up to the surface between the zooid-cavities, and between these and the polyp-cavities.

Z. Zooids.
PM. Protractor muscle.
RM. Retractor muscle.
C. One of the canals of the transverse system.

Fig. 3. Transverse section across a polyp of *Heliopora cærulea*, taken just below the mouth (decalcified). The tips of four of the tentacles cut across are retained *in situ*; the other four have fallen out.

D. External layer of connective-tissue cells.
C. Layer of homogeneous connective-tissue giving off a series of stout offsets (A), which pierce the layer (D) and project externally. This layer is seen to form the central plate of the mesenteries and a wall around the stomach.
EN. Entoderm lining the whole of the intermesenteric chambers.
M. Mesenteries.
RM. Retractor muscles. The "Dorsalfach" of KÖLLIKER lies below in the drawing, the "Ventralfach" above. The muscles are covered by the entoderm.
TT. Tentacles cut across.
S. Stomach. B. Its muscular layer.

Fig. 4. Section parallel to the surface of *Heliopora cærulea*, to show the relation of the hard parts to the soft.

TC, TC and the similar oval spaces represent tubular cavities of the cœnenchym cut across. The interspaces between these cavities are occupied by the hard tissue.

The hard tissue is fibrous in structure, the fibres radiating from a series of axes here seen cut across (C). Suture-like lines (S) occur occasionally where the peripheries of the various radiating systems join.

D. Layer of connective-tissue cells.
C. Layer of homogeneous connective-tissue.
EN. Entodermic layer.

Fig. 5. Polyp of *Heliopora cærulea* and the immediately surrounding structures as viewed in a thick horizontal section from the outer surface.

The outer epithelial layer is not seen, being too transparent. The superficial projecting points of the hard tissue of the corallum are opaque, and are shown shaded dark. Away from the calicle the points are arranged in parallel rows. All over the surface are seen the tops of the ramifications of the superficial system of canals or sinus (V, V, fig. 1); those immediately around the polyp-lobes have a radiate arrangement. These canal-cavities are lined with entodermic cells.

In the centre of the drawing are seen the eight lobes of the contracted polyp with the mouth of the atrium in their centre. In their peripheral region the entodermic lining of the cavities of these lobes is seen showing through their superficial tissue.

Each of the lobes further shows a fine longitudinal striation, probably caused by muscular fibres, and very small nuclei at its inner aspect.

P. Projecting points of the corallum.

AA. Sinus of the superficial canal-system.

L. Lobes of contracted polyp.

Fig. 6. Portion of a section of *Heliopora cærulea* parallel to the surface and viewed from beneath. From a specimen decalcified in chromic acid. The drawing represents a spot where a growing point of the corallum has been removed by the acid.

EN. Entodermic layer.

C. Homogeneous connective-tissue layer.

D. Layer of connective-tissue cells.

B. Very finely fibrous mass from which the calcareous tissue has been removed.

A. Cavity in the mass.

PLATE 9.

Fig. 7. Diagram to show the canal-systems in connexion with the summits of the cœnenchymal tubes and calicles.

A. Cavity of a calicle.

B. Cavity of a tube.

D. Walls of these in longitudinal section.

The canals of the deep system (V, V′) lead over the summits of the walls from one tube to another, and from the tubes to the calicular cavities. The canal (V′) opening into the calicular cavity in the figure corresponds to the opening (O) in fig. 8.

C. A similar canal leading into a tube behind B.

Above is seen the superficial canal-system, consisting of smaller canals and sinus communicating with the deep canals and roofs of the cœnenchymal

tubes and laterally with one another. They have usually a vertical course. Their summits are seen in Plate 8. fig. 5.

Fig. 8. Transverse section through the uppermost part of a retracted polyp of *Heliopora cærulea*, as viewed from below, showing the under surface of the most superficial structures closing the mouth of the calicle, *i. e.* the immediate under surface of the polyp-lobes seen in Plate 8. fig. 5 and Plate 9. fig. 7. The drawing is from a decalcified preparation. The soft parts lining the wall of the calcareous calicle are cut through; they retain the form of the calicle, to which they were closely applied. The wall presents a series of longitudinal folds so as on transverse section to show a sinuous outline with twelve indentations separated by twelve bulgings. The indentations occupied in the fresh condition of the animal by calcareous matter represent the twelve ridge-like calcareous septa present in the calicle. The indentations are neither in form nor arrangement symmetrical, nor are the eight mesenteries (M M) arranged symmetrically with regard to them.

Between the mesenteries the body-wall of the polyp does not reach outwards everywhere the entire distance to the wall of the calicle, but is continuous with this only in the region of its indentations. At each of the bulgings of the wall a wide aperture is left, by which the cavity of the polyp communicates with the canal-systems around.

M M. Mesenteries.

O O. Openings by which the polyp-cavity communicates with the canal-systems. The light oval spaces shown in the shaded areas of the openings are the sinus of the superficial canal-system.

Fig. 9. Vertical section through one of the zooids of *Sarcophyton*. On the left-hand side of the drawing the calcareous spicules are shown *in situ*. On the right the appearance presented after these have been removed by acid is shown.

The points of the spicules accompanied by a layer of connective-tissue project up far into the epithelial layer, raising it up just as the points of hard tissue in *Heliopora*. The connective-tissue shows excessively small ramified cells scattered through its otherwise homogeneous tissue. Portions of adjacent zooid-cavities are shown on either side of the central one; the transverse fibrillation of their wall is indicated.

Sp. Spicules.

S.C. Cavities from which spicules have been removed by acid.

S. Stomach of zooid provided within with long cilia directed inwards.

ME. Its mesenteries.

MF. Mesenterial filaments.

C. Canal of the transverse system, forming a communication between two adjacent zooid-cavities and lined by entodermic cells continuous with the layers lining the zooid-cavities.

EN. Entoderm.

C. Canal cut transversely.

Fig. 10. Portion of the superficial structures of *Heliopora cærulea* as viewed in a thin vertical section.

E. Ectoderm, consisting of elongate club-shaped cells running out below into fine processes, which traverse the next succeeding layer (M) of homogeneous connective-tissue. At the bases of these cells are cells of similar structure but irregular form. Small nematocysts lie amongst the epithelial cells, and some of them (N) are shown in the deeper regions. At EN the wall of one of the tubular cavities of the cœnenchym is seen in section at its edge, showing its three layers and the residue of animal matter (P) left by parts of its calcareous wall after decalcification.

Between EN and the section of the wall of the canal (V′) a narrow strip of the inner surface of the tubular cavity is viewed from its surface aspect.

E. Epithelial layer.

M. Layer of homogeneous connective-tissue.

N. Nematocysts.

C. Connective-tissue cells.

V. Canal of superficial system.

V′. Canal of deep system.

EN. Entodermic cells.

D. Layer of connective-tissue cells.

P. Residue of tissue after decalcification of a portion of the wall of a cœnenchym-tube.

Fig. 11. Section vertical to the surface of the corallum of *Heliopora cærulea*, showing the structure of the hard tissue.

A. Former calicle-cavity shut off from A′ the recent calicle of the tabula, C.

The tube-cavities on either side have similar tabulæ developed in them. In some of the tubes their walls are shown as cut parallel to their surfaces, in other places the cut edges of the walls only are seen.

The tabulæ being applied against the already formed insides of the calicles and tubes as a later formation, the line of the old wall of the calicle can always be traced up for some distance past the level of the tabula, which appears as the bottom of a second tube fitted within the first. The fibres forming the walls of the tubes &c. are inclined upwards and outwards at a uniform angle from the vertical axes.

A. Former; A′, recent calicular cavity.

C. Tabulæ.

B. Portion of wall of tube cut parallel to its surface, showing a line of suture between the fibres of opposite systems composing it.

D. Vertical canal.

P. Point of growing coral, showing lines of successive growth.

The numbers indicate the order in which the successive chambers were formed.

Fig. 12. Portion of the hard tissue forming the wall of a tube-cavity of *Heliopora cærulea*, from the same preparation as fig. 11, more highly magnified.

C. Axis.

B, and similar shaded bands on the other side of the axis. Part of the tissue stained of a more intense blue than the remainder.

Fig. 13. *a*, *a*. Two of the cells of the entoderm of *Heliopora cærulea*; one of these with the contents undergoing fission.

b'. Nematocysts of the same.

b. A form in which they are commonly to be observed, with the thread partly protruded and curved in a loop, and with one side of the cell bulged in.

Fig. 14. Ovum of *Heliopora cærulea* as attached to the mesentery.

Fig. 15. Diagram to show the growth of *Heliopora* by successive budding and development of tabulæ.

A. The original calicle of the stock: A′, A″ &c., successively formed chambers in continuation of this calicle; 1, 2, 3, successive buds.

B. Formation of a new calicle. A short tube buds out, but the tubes on either side of it grow more quickly. Only the outer part of their walls continues to be developed; hence a wide calicular cavity is formed with the original short tube at its bottom.

Fig. 16. Drawing by Mr. J. J. Wilde, Artist to the 'Challenger' Expedition, of a rapidly growing tip of a frond of *Heliopora cærulea*.

The young growing tubes of the cœnenchym are polygonal in area.

A A. Calicles in various stages of formation.

Fig. 17. A calicle nearly fully developed, as seen when looked directly into. The calicle is surrounded by irregular dentations, of which there are more than twelve. A circlet of cœnenchymal tubes is seen to join the cavity of the calicle below.

V. *On the Development of* Lepas fascicularis *and the* "Archizoëa" *of Cirripedia.*

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Burmeister's important discovery that in *Lepas* the larvæ pass through a *Nauplius* and a *Cypris* stage was made on the same *Lepas* which forms the subject of this paper. Burmeister*, however, had evidently only a ball of this *Lepas*, some specimens of which were young in the *Cypris* stage, which had just settled; while others were dismissing young *Nauplii*, which, unless great care is taken, die very soon in captivity. He thus missed the intermediate stages, which, however, were at that time much less important, as the first thing that was wanted then was to establish the general outlines of the Cirriped development. The *Nauplius* of this *Lepas* has since been seen by Darwin†, to whom Hancock showed it, "calling his attention to a proboscidiform projection on the underside of the larva of *Lepas fascicularis* when just escaped from the egg."

Neither J. v. Thompson's nor Pagenstecher's observations refer, as far as I can find out here, to *Lepas fascicularis*; and it seems not to have been taken up again as an object for embryological researches until Claus published his paper on the *Cypris*-like larva (pupa) of the Cirripeds and its metamorphosis into the fixed animal (Marburg, 1869), a paper of which I have unfortunately only an abstract, as given by Nitsche in his embryological report for the year 1872, and by Claus himself in his 'Grundzüge der Zoologie,' which, however, affords nearly all the information necessary for my purpose. My object is to give an idea of the whole development of one *Lepas* as accurately as possible, which seems never yet to have been done, as our whole knowledge of the development of this group consists of fragments, collected mostly in the same way in which Burmeister gained his information.

The materials for this paper were obtained during our cruise from Japan to Sandwich (June to July 1875), as we went along the thirty-fifth degree of latitude, when first very curious *Nauplii*, some of them 12 millims. long, were caught, which I identified at once with the nauplial form to which Dohrn has given the generic name of *Archizoëa*‡. In

* 'Beiträge zur Naturgeschichte der Rankenfüsser,' 1843.

† 'A Monograph of the Subclass Cirripedia: The Lepadidæ.' London, 1851, p. 11.

‡ Dohrn, "Untersuchungen über Bau und Entwicklung der Arthropoden. IX. Eine neue *Nauplius*-form (*Archizoëa gigas*)," in v. Siebold und Kölliker's Zeitschrift für wissenschaftliche Zoologie, Band xx. p. 597, 1870.

the daytime these larvæ were scarcer (many of them came up, however, from a depth of 60 fathoms), but at night they were so common that large bottles could be filled with them. The question (which had been left open by Dohrn) to which Cirriped these extraordinary *Nauplii* might belong, presented itself of course again to us, and we tried to obtain all the Lepadidæ we could. In a day or two we got into large streams of floating Lepads; and now it was an easy thing to get as many as we liked, and to bring up in our globes such stages of the large *Nauplii* as had also been taken by us on the surface, and which clearly belonged to them. Then, again, when catching large quantities of larvæ, we got among them (especially when the net was skimming the very surface of the water), (1) some which were ready for the metamorphosis into the *Cypris* stage, (2) the *Cypris* itself swimming and creeping about or just settled on a dead *Velella*, and (3) the stage in which the *Cypris*-shell is about to be thrown off, in order to make room for the growing valves of the young *Lepas*.

The species to which this barnacle belongs is decidedly the very variable *Lepas fascicularis* as described by Darwin, *l. c.* p. 92. The formation of the balls, the brittleness of the shell, and the peculiar shape of the valves show this at once; there are, however, some differences which must be mentioned in detail, as possibly this North-Pacific species deviates from the Atlantic one not only by these small differences, but also by possessing another nauplial form, in which case it would be decidedly necessary to separate this Pacific form from it. In most specimens which I dissected I found six teeth in the mandible, not five, as is the ordinary number. Sometimes, however, there are five on one side and six on the other, as in the case which I have figured (Plate 15. fig. 30, *a* and *b*), showing that this difference has no constant value. The maxillæ have sometimes four steps (the regular number as given by Darwin); but they have more commonly only three steps besides the two large, unequal, upper spines (fig. 29). These are the only differences from an ordinary *Lepas fascicularis* which I can find; and they merely show that this Pacific form is a variety of the Atlantic one, in case there should not be a difference in the development of the two. As we know, however, nothing about the five stages through which the Atlantic form has to pass if it follows the same mode of development as this one, and as no "*Archizoëa*" has as yet been described from the Atlantic, this question must remain an open one until further information.

I will now proceed to give an account of the development of *Lepas fascicularis*, mentioning the publications which refer to certain phases, in their respective paragraphs.

I. *Development of the Egg and of the youngest* Nauplius.

The ovarium, a cellular body at the top of the pedunculus, has a light bluish colour, as in all Lepadidæ. It consists of tubes and their cæca, in which we find the ova in a more or less advanced state of development. In a young specimen one finds the ova sometimes in different stages, but in the older ones nearly all the ova in the ovary (with the exception of those "mother cells" which do not develop) are in the same stage of

development, as are also those contained in the lamellæ. In *Balanus* the ramified cæca of the ovarium show ova in different stages of development. According to Buchholz*, who saw the youngest ova in the cæca, and describes them as transparent small vesicles with a germinal vesicle and a nucleolus (exactly the same as may be seen in the tubes of *Lepas fascicularis*), these vesicles grow as well as the ova—a statement which, I think, may also be made for the latter. As these vesicles grow they are more and more filled with yelk-granules, until the vesicle is no longer visible and only the nucleolus is seen as a clear spot in the centre of the ovum (Plate 10. fig. 3 and fig. 1, *n*). Evidently the shell round these ova is not yet formed, as they are soft and change their form according to their position in the ovary. Among these large developing ova you may see in this stage small transparent cells, with a vesicle and a nucleolus (fig. 3, *oi*), which do not take up any yelk-granules, and which are, I think, the mother cells from which the next set of ova will be derived as soon as this one has advanced into the ovarian lamella. I looked of course for such cells as have been described in *Sacculina* by Van Beneden†, but never saw any of them budding; nor did I ever see those "cellules accolées" on one of the poles of the growing ovarian cell which he has described. They must be peculiar to the latter genus, where they have been seen by Gerbe as well as by Van Beneden, while in *Balanus* Buchholz seems not to have remarked any thing of the kind.

In our species I think the small cells divide by budding, and give rise to more small ova, which have the same form as the mother cells, and afterwards grow in the way which has been described above.

The spermatozoa are hair-like filaments, which offer no special character (fig. 3, *a*). I have, however, not studied their development.

After the last-described stage (Plate 10. fig. 1, *n*, and fig. 3) the ova leave the ovarium and get into the ovarian lamellæ, which may be easily found on both sides of the body. How they get there has been a subject of much speculation. Krohn's theory of Darwin's auditorial sac being the orifice through which they have to pass, seems to me to be the most likely one; but only carefully done sections of mature specimens will be able, I think, to solve this question, which is not an object of the present inquiry. The ova, as we find them in the lamellæ, are ellipsoidal. They have acquired a shell during their passage through the oviducts, and show no trace of the nucleolus vesiculæ germinalis. They have in this stage a length of 0·26 millim.

Burmeister thinks that each of the lamellæ contains about 2000 ova. He also figures some ova, which, judging from their shape, are later stages in which the embryo begins to be visible within. The mature ovum is entirely filled with granular

* J. Münter und R. Buchholz, "Ueber *Balanus improvisus*, Darw., var. *gryphicus*, Mütr." Berlin, 1869. An abstract is given in Grenacher's Report for 1869 in Henle and Meisner's 'Bericht,' &c. (Leipzig, 1871), p. 424.

† "Recherches sur l'embryogénie des Crustacés. III. Développement de l'œuf et de l'embryon des Sacculines," Bull. de l'Acad. Roy. de Belgique, 1870.

yelk-cells, only in the middle some small bodies may be seen reflecting the light very strongly, and looking like minute granules of fat (Plate 10. fig. 4).

About the formation of the embryo there are, or at least there were, two opinions, the one backed by Fritz Müller, and for some time (according to Van Beneden) also by Claus, maintaining that a total segmentation takes place, and that the embryos are developed in full without a preceding "Primitivstreifen," which means a larger gathering of cells on the ventral side of the embryo*, while Van Beneden has seen and figured the latter in *Sacculina*.

Buchholz mentions, like Van Beneden, the formation of the blastoderm, but does not seem to have seen a primitive streak. According to him one of the two halves, which are the result of the first segmentation, divides again, and its segments overgrow the other half, forming a blastodermic cuticle round it, in which grooves may soon be seen, indicating the future position of the three appendages.

Lepas fascicularis is not a very favourable object for such an inquiry; nevertheless I have arrived at a result which holds somewhat an intermediate place between Van Beneden's and Buchholz's observations. I saw the blastoderm forming very much in the way described by the former, but I was unable to find any definite trace of a primitive streak. The first alteration which takes place is the formation of two segments (fig. 5, where a small third one may be seen between the two), which are unequal in size, whereupon the lower and larger one divides again (fig. 6). In these stages of segmentation you see already two to four large, transparent, nucleated cells, which separate themselves from the yelk-globules in the middle of the ovum, and the number increases very much in the next stage (fig. 7). We find first eight and then twelve. In fig. 7, *y*, *x*, I have given a sketch of two sorts of cells which are now contained in the ovum, and which, after breaking its walls, can be separately inspected: these are large blastodermic cells with a single nucleus, with only a few granules, and small, very granular yelk-globules. Also in Van Beneden's drawing I do not find a stage between the mulberry stage and the stages of first segmentation; and I must confess that in *Lepas fascicularis* I never could find but indistinct traces of the later stages of segmentation. The large cells seem to break out and include the rest of the yelk, thus forming a blastoderm (fig. 8) consisting of small nucleated cells. This was well enough to be seen with reflected light; but the interior of the ovum is so little transparent that I could not make out whether there is a primitive streak on one side or not. The blastoderm now loses its cellular look, and has the appearance of a granular cuticle, just as it has been seen by Buchholz in *Balanus*; and then a groove, which was already visible in the last two stages, is seen to become deeper, and on each side of it the first traces of the three pairs of appendages (fig. 9, *a* and *b*) become visible. Very soon the labrum also appears; the tail is differentiated, and setæ may be seen at the top of the foot-joints (fig. 10). In *Sacculina* the embryo throws the egg-shell off before this happens, and is instead (according to Van Beneden)

* Fritz Müller, 'Für Darwin,' 1864, p. 64.

contained in the enlarged blastodermic cuticle. In our case I have not been able to make any observation of the kind, owing perhaps to the circumstance that in every *Lepas* one finds all the ova in one and the same stage of development, which makes it very difficult and laborious to get at all the different stages. The circumstance that the cuticula (whether egg-shell or blastoderm) which contains the embryo is larger than the ova were (0·29 millim.) is perhaps in favour of such a moulting as has been observed in *Sacculina*, but might also be explained by a certain elasticity of the egg-shell. We find such a case in worms, where, for example in *Distoma megastomum*, the shell is considerably extended*. When working out the first development of that Trematod, I have already remarked that something very like it has been observed. The same thing has been found in *Distomum veliporum* by Guido Wagener, in *Pteromalines* by Ganin, and finally in *Balanus improvisus* by Buchholz. And as in every other respect the first development of *Lepas* has been found to be so similar to that of *Balanus*, I am inclined to think that it is also in this case the egg-shell which the embryo leaves, and not the blastodermic cuticle, which very likely still adheres to the young *Nauplius*.

II. *The successive* Nauplius *stages.*

The *Nauplius*, when escaping from the ovum (Plate 10. fig. 11), has a length of 0·35 millim. It has been figured by Burmeister, but evidently (if it is at all the same as ours) as seen under a very low power, and without giving many details. I do not know whether, judging from this figure, one has a right to state that the variety of *Lepas fascicularis* at which he has been working is the same as ours or not. This being also the case with the figure of the *Cypris* stage, it is unnecessary for me to refer again to his paper, the object of which was more to show that such larval stages existed in Cirripedia, than to give details about their organization.

We saw these embryos in our globes as soon as a ball of *Lepas* had been put into them. At this time of the year there are in every bunch some specimens which continually dismiss from their ovarian lamellæ large numbers of embryos. These swim slowly about, until they undergo their first metamorphosis, which consists in casting off a very thin skin enveloping their body and in pushing out their tail and their caudal spine, which, enclosed by that cuticle, have hitherto been pushed in like the tubes of a telescope and unable to extend to their full length (fig. 11, and fig. 11 *b*). I was at first, when I had not noticed this cuticle, very much puzzled by this; for I saw that the tail ended in two spines, and the caudal spine in a single spiny process. When, however, the covering-glass had been pressing a little on the embryo, I noticed a long tail and a long caudal process, the longer the more it had been forced out from the animal's body by the pressure exercised upon it; then I discovered in animals which were perfectly unhurt the cuticle which envelops the animal's body, and which is also clearly visible at the

* "Ueber einige Trematoden und Nemathelminthen, von R. v. Willemöes-Suhm," Zeitschrift für wiss. Zool. Bd. xxi.

end of the lateral horns. These are in the young embryo not yet erected, but still hanging down. On the extremities of the appendages, however, I observed nothing of the kind. They are three in number (fig. 11, *a*, *b*, *c*), and indicate already all the peculiarities which will be described in the full-grown *Nauplius*, and which in this stage can best be understood from the figure. The upper lip (fig. 11, *la*) is already plainly visible; and, apparently, also the œsophagus, on both sides of which we find a group of cells in the place where we afterwards see two glands, which perhaps lead into the stomach. The intestine shines through the body of the larva, in which there are as yet a great many yelk-granules, which prevent you from seeing the intestines, upper and lower portion.

The first change is undergone by the *Nauplius* very soon after it has left the ovum. In a globe into which I had put a ball of barnacles, and in which at first all the larvæ were in the stage just described, I had some difficulty in finding any of them half an hour afterwards, as the greater number had already cast off the cuticle, pushed their tails and spirals out, and erected their horns. I have been thinking whether this cuticle is not perhaps the blastoderm adhering to the embryo, which leaves it very much as a *Botriocephalus* embryo leaves its ciliated larval skin. For reasons which I have given when describing the development within the ovum, I am, however, not quite sure about this, and shall only be able to decide the question when I have studied other Lepadidæ which may be caught on the surface during the progress of our voyage. In the first *Nauplius* stage I saw a lens above the eye (fig. 11), which I did not, however, see in every case when I looked for it, and which in the later stages was seen no more.

After the first moulting the embryo has grown very much, having already a length of 0·6 millim., but showing only few differences in its organization, as all the spines on the tail, and especially the first two movable ones (Plate 11. fig. 13, *sp*), existed previously. At the end of the lateral horns we do not yet find those fine hairs which distinguish the later stages, but only a few small setæ and a larger one (fig. 13, *cp*). Muscles are seen running up to the horns; but the glandular system which is beginning to form inside the body, indicated by small granulated cells, is not yet in connexion with them. In the upper lip, the sides of which are covered with fine hairs, indications of the teeth may be seen; but as yet the whole of the intestinal tract shows no progress, except that the anus is now clearly visible. On both sides of the eye we find two tentacles, well-known sense-organs the function of which is very doubtful and likely to remain so.

The carapace shows as yet no protuberances, with the exception of the lateral horns and two small spines at the base (fig. 13, *z*). In the appendages the setæ are very much larger, especially the one which springs from the segmented ramus of the third pair, which is as long as the tail itself. After the larvæ had reached this stage in our globes they invariably died, which has also very likely been the case with those of former observers, as nobody seems to have ever seen the very interesting (*Archizoëa*) stages which I am now going to describe, and which were found on the surface with the

preceding ones. There is accordingly no doubt about their being stages of the development of one and the same animal. This, besides, is shown clearly enough by the similarity in the tail, its spine, and the labrum of the two forms, which have been figured on Plate 11.

Before I give, however, the description of the stages through which the Cirriped has now to pass, I must explain the name *Archizoëa*. It has been given by Dohrn to a *Nauplius* which has a length of 4–5 millims., a height of 1½–2 millims., and has the shape of a Chinaman's hat. It has a large caudal spine and a dorsal one, six movable spines on the tail, besides many fixed ones, a large labrum, and a very spiny caparace. These *Nauplii* have been caught off the coasts of Chili, and been described by Dohrn in a most perfect way. Why, however, he gave to it a generic and a specific name, though he clearly knew that it was a Cirriped *Nauplius*, I do not know; for he could have published his ideas about the "complete *Zoëa*, which as a perfect larval form has vanished from the development of Cirripeds," and the remains of which may be found in the dorsal spine and perhaps in some movable spines on the tail, without doing so. I have also caught the larvæ which he has called *Archizoëa gigas*, and may at once add that I have good reasons to believe them to be the *Nauplii* of *Lepas australis*. Thus I was able to study these two different forms alive, and have come to the conclusion that they are true *Nauplii*, and have nothing whatever to do with a *Zoëa*. "*Archizoëa gigas*" has a length of 4–5 millims., and is chiefly distinguished from our *Nauplius* by the shortness of its spines, the multitude of gland-openings in processes (spines) all over the carapace, and by the number of spines on the labrum (five on each side, in our case two). I got some specimens from the surface off the southern coast of Australia, which I believe to belong to *Lepas australis* for the following reasons:—*Lepas fascicularis*, to which undoubtedly our *Archizoëa* belongs, is (to use Darwin's words) "certainly much the most distinct of any in the genus; and Mr. Gray has proposed to separate it under the name of *Dosima*; but considering the close similarity of the whole organization of the internal parts, together with the transitional characters afforded by *L. australis*, I think the grounds for this separation are not quite sufficient." And in describing *Lepas australis* he says, "this species has some affinity to *L. pectinata*, but it is much more closely related to *L. fascicularis*. I believe this species is confined to the Southern Ocean, and perhaps there represents *L. fascicularis* of the northern seas." Now larvæ which are very nearly allied to those of *L. fascicularis* have been found in the Southern Ocean; and it seems to be almost certain, after what has been said about the relations of *L. australis* to *L. fascicularis*, that the *Nauplii* in question belong to the former species. This is all the more probable as the pupa stage of *Lepas australis*, which has been described by Darwin as having a length of 2–3 millims. (0·067–0·1 of an inch), corresponds in size to the large *Nauplii* described by Dohrn, and resembles very closely in all points of its organization the pupa of *Lepas fascicularis*, which I am going to describe below. We ourselves caught these large *Cyprides* of *Lepas australis* and the young barnacles of the

same species together with those *Nauplii* when we were south of Australia; but I had unfortunately not examined at that time the first stages of *Lepas australis*, which would doubtless have led me to the young "*Archizoëa*." However I have a good chance as we go through the straits of Magellan to get them again, and hope that I shall have the embryos of *Lepas australis* in our globes.

I shall now proceed with the description of our larvæ.

After the second moulting (or the third if one counts the throwing-off of the thin cuticle) two great changes occur which totally alter the look of the *Nauplii*. In the first place we find on the back (which was hitherto somewhat conical, but had no protuberance) a large spine (Plate 11. fig. 14, *ad*), which has already very nearly the length of the caudal one, with which it is now growing in equal proportion. In the second place the carapace, which formerly exhibited only two small spines (figs. 13 & 14, *z*), shows now six acute processes, two of which are situated in the front line between the two horns, and two others, a smaller and a larger one, on each side. These processes are not spines, in so far as they are not closed at the top; they have an opening there, and the chitinous substance is pushed in a little into them up to the point where it meets the duct of the glands, which are to be seen at the base of all these processes.

These glands are as yet unicellular, the same as they were in the last stage. Dohrn says, in describing his *Nauplius*, that he suspects the ramified glands to have been preceded by unicellular ones—a supposition which is borne out by the facts. The appendages show as yet no change, nor do the tail and its spine, in which there are as yet only two of the large secondary movable spines (Plate 11. fig. 14).

On both sides of the eye, between the two tentacles or feelers, there is a granulated substance, which I thought at first was the brain; but afterwards I found the ganglia underneath it (fig. 14, *cer*), and have never been able to make out what this granulated band represents.

The upper lip now not only includes the œsophagus, but also two glands or cæca (fig. 14, *coe*), in the place of which we saw in the last two stages an assemblage of slightly granular cells. There are now two strong spines on both sides of the edge of the labrum, which has very much the form which it retains during the whole *Nauplius* stage.

Also the top of the lateral horns (fig. 14, *cp*) has changed. We find two pointed chitinous prolongations, and between them a great many fine setæ occupying the edge of the rounded margin. The dimensions of the embryo in this stage are as follows:—

	millim.
Width of carapace	0·25
Length of cornua parietalia	0·21
Length of carapace	0·32
Length of tail	0·66
Total length	0·98
Width of frontal line	0·11

The young *Nauplius* is now in full vigour, evidently taking in plenty of food and rapidly growing. Every time it moults it gets one more movable spine on the tail (Plate 12. fig. 15, sp^1), on which there is, a little lower down, another large curved spine (sp^2), and lower down still a straight one, besides a number of small and middle-sized spines. In the full-grown *Nauplius* (the carapace of which has a diameter of 2 millims., and the larger spines are 12 millims. long) there are *six* movable pairs of spines on the tail. It gets these only after the fifth moult, the last it has to undergo in the *Nauplius* stage of its life. The number of spines is the chief test of its age, and will be found to correspond exactly to its size. When in possession of three or four of them it is only half the size of one which has six. After this, however, it in most cases gets six spines at once. I have figured in the accompanying Plates two stages—one with four and the other with six spines, and have represented in each of these figures different organs so as to show its anatomy without crowding them too much. In giving a description of the *Nauplius* in the adult stage, I shall of course frequently refer to the "*Archizoëa gigas*," but must first mention that DOHRN, though his figures of the three appendages are excellent, has evidently taken the second for the third appendage, so that in comparing our drawings with each other this must be borne in mind. When I remarked it, I looked at the *Nauplii* of both species again, to see whether I had not perhaps myself made the mistake (which, as one separates the appendages from the body, is very excusable); but I found that certainly my drawings are correct, and that of all the appendages the second (as is also the case in the *Nauplii* of several other Cirripeds which I have studied) are the largest.

The carapace of this *Nauplius* has the form of an hexagonal cover, with a very long handle to it springing from its middle, which is a little raised (Plate 10. fig. 12). Besides the central spine there are on the carapace two posterior lateral processes, two processes in front of the eye between the horns, six large processes (one at each angle of the hexagon), and several smaller spines (two to four) between each pair of these. Altogether there are on the carapace one dorsal spine, two lateral horns, eight larger, and from twenty-five to thirty smaller processes, all of which, with the exception of the spine, have a gland opening at the top.

In "*Archizoëa gigas*" there are also eight large processes (*vide* DOHRN's fig. 1 on tab. 28, *l. c.*, and my fig. 23 on Plate 14) with glandular openings; but besides there are a vast quantity of very small spines between them, covering the whole upper surface of the larva and the margins of its carapace. The greater part of these, or rather all, with the exception of some small hairs or hair-like spines, have openings at the top, and ducts from the glands, which densely fill the whole carapace, may be easily seen running up to them.

The dorsal spine is movable, and a large muscle may be seen running into it. This has been represented in Plate 12, for which I have on purpose taken a specimen which was soon going to moult, and in which the muscles inside the large spines have grown so much that they cannot stretch out, but are obliged to coil themselves up.

The lateral horns (Plate 13. fig. 17) are said by Claparède and Buchholz to be movable. In our case they certainly are provided with muscles, running up to them from the dorsal centre of the carapace, and fixing on a chitinous ring which looks like a septum in the upper portion of the horn (Plate 13); but I have never seen a movement in these horns, though I examined many living specimens. Their outer chitinous covering is inverted at the top (where it has two prolongations and many setæ attached to it), and runs inside up to the place into which the glands pour their contents, and which is also the place of attachment for the muscles (fig. 17, *q*). Here two large glands and two smaller ones terminate. Whether these large glands, the bottoms of which are fixed to the carapace by threads of connective-tissue, are in communication with the general glandular system of the carapace I doubt, as I never saw such a communication. With all the smaller glands, however, which run up to the different processes (fig. 16, *gl* and *pr*, fig. 17, *pr*, and fig. 22, *gl*), this is undoubtedly the case; they form a large glandular network all through the carapace, just as Dohrn has already described in *Archizoëa gigas*.

On the lateral horns we remark a few very small spines, the only spines which have not a gland opening at the top.

A question which has been left open by Dohrn is the innervation of these different organs, about which he could say nothing, having only spirit-specimens at his disposal. I have examined the larvæ alive under the highest power, and have arrived at the following result. The only exterior appendages, which are very likely sensitive, are small reflecting hairs (figs. 16 & 17, *y*), to the base of which runs a somewhat varicose nerve-fibre. No sensitive appendages are to be found at the top of the lateral horns nor of any of the processes. The glands, however, are in connexion with nerves, and it is by no means difficult to find nerves sending off branches in all directions. One may trace these easily to the base of glands which terminate in the larger processes. In one case (fig. 16, *c*) I have also seen a ganglionic cell close to one of these processes, sending apparently a fibre up to it, but not being connected with the large lower nerve (fig. 16, *n*) which gave a branch to the gland.

Neither the small nervous hairs nor the innervation of the glands is at all extraordinary, as in many of the lower animals, which are favourable objects from their transparency, something of the same kind has been observed.

Dohrn, when speaking about these lateral horns, says that as Claparède and Buchholz have declared them to be movable, and described muscles running up to them, and as on the other side the evidence given for a transformation of the first appendages into the antennæ with the sucker seems not to be sufficient, he is inclined to think that these organs are modifications of the lateral horns. He adds that they must have a very important function, because otherwise their complicated structure would not be intelligible. Nevertheless my observations, as I shall show below, make me think that Krohn, Mecznikow, Pagenstecher, and Claus, who maintain against Burmeister and Darwin the first-mentioned way of metamorphosis, are perfectly

right, and that the lateral horns have nothing to do with the antennæ of the *Cypris*. For what reason all these glands terminate in the two horns and their processes is another question, to which I can give no answer. The secretions of these glands during the *Nauplius* stage may be continually seen coming out of them; in the *Cypris* all these processes have been dropped, and the gland appears as a shell-gland; and later, when the *Cypris* has fixed itself, this shell-gland, I think, is the one that furnishes the materials for the valves.

The centre of the nervous system consists of two ganglia, which may be seen below the central eye, but which are often somewhat hidden by the upper part of the lip (Plate 13. fig. 18, *cer*). Above them, between the pigment-spot and the two feelers, there is a dotted band of a substance which might be nervous, but about the nature of which I am not able to give an opinion.

The *feelers* (Plate 13. fig. 18, and Plate 14. fig. 22, *x*) consist of a basal joint, to which muscles are attached, and of a flexible upper one, into which a nerve goes. At their top I found no special terminating bodies, though I examined them repeatedly under high powers. These feelers are movable in a limited way.

When the *Nauplius* has moulted for the seventh time, and the time for the metamorphosis into the *Cypris* stage arrives, we see the large lateral eyes in the process of formation. At first they are a pair of roundish bodies (Plate 14. fig. 22, *o*) reflecting the light and dotted with black pigment. Very soon the black pigment becomes more intense; about eight lenses appear at their surface, and above each lens a cornea is formed. This stage is figured in fig. 23 for the southern larva, but is in our case so similar that I did not think it necessary to give another figure for it. However, it takes a long time to find a specimen among the largest larvæ which have got these eyes, as they seem to throw off their Nauplial appendages as soon as the preparations for the metamorphoses are ready underneath. Among all the larvæ which I examined I found only one in the stage figured on Plate 14; but I have no doubt that many might be discovered among the vast quantity of larvæ which have been kept in our bottles.

The organ *y* (Plate 14. fig. 23) is not, as may appear at first sight, a ganglion, but a patch of vesicular tissue, of which several may be seen in a specimen which has been killed in absolute alcohol and preserved in Canada balsam. The glandular substance in this specimen (easily recognizable from being more stained by carmine than the surrounding tissue) has been somewhat contracted, and patches of vesicles have appeared which clearly belong to a network of connective-tissue between the glands.

The *labrum*, which in Plate 12. fig. 15 is represented as turned upwards, and in Plate 14. fig. 22 in the position in which the larva generally keeps it, is a very long and wide organ, being nearly two thirds of the diameter of the carapace in length. Its edges are very densely covered with small spines, and at the top there are invariably on each side two large spines. In older larvæ, however, I frequently saw three spines (fig. 15), and in one case even four on both sides. It resembles on the whole very

much the labrum of the southern larva, in which, however, there are five large spines and three small ones on each side.

At the top of the labrum is the round opening for the mouth, leading into an œsophagus which runs through the middle of the labrum. At the point of attachment this œsophagus is covered by a large pigment-spot (fig. 15, *pi*), on both sides of which two glands are seen, which first seemed to me to run into the stomach (fig. 15, *coe*); but afterwards I could never find any communication between the two, and I am very much inclined to see in these two glands those which in the *Cypris* are to be seen close to the stomach, and which send their ducts up into the antennæ. Dohrn has seen these glands, but has not been able to identify them as such, as his specimens were rather badly preserved.

The œsophagus leads into a stomach, or stomachial intestine; for the stomach is not so strictly separated from the intestine as might appear from fig. 15, which, however, is quite correct, in so far as in animals which are alive there is a strong constriction to be seen. Especially the upper portion is covered with a strongly pigmented epithelium, which in our drawing (fig. 15) has come out a little diagrammatically, as in reality the hexagons are not so regular as they appear there. I found the upper portion of this intestine filled with small algæ allied to coccoliths &c. In the lower portion the pigment of the cells is less intense, which makes it appear more even, less dark, and of a light brown colour. The *intestinum rectum* is, as a rule, filled with granulated excrements, and leads to the anus, which may be easily discovered by getting a side view of the tail between it and the caudal spine (fig. 15, *as*). On both sides of the rectum there is a glandular coating, and another larger gland, which is enclosed in the tail (fig. 15, *gl*), is seen to go into the lower portion of the intestine.

Both the tail and the large caudal spine get their muscles from the upper centre of the carapace, where they are attached near those of the dorsal spine.

The caudal spine is covered, like the dorsal, with recurved spines. In old *Nauplii* this spine is more than double the length of the tail. Between the two there is a bunch of red feathery hairs, just in the same place where three such hairs have been described by Dohrn (see his pl. 29. fig. 6). Here there are four of them, one of which is very much longer than the others.

In the tail (Plate 12. fig. 15, and Plate 14. fig. 22) we find (1) six pairs of movable spines, each of which has muscles running to it; (2) somewhat lower down a pair of spines which are not movable, but recurved; (3) a pair of large, nearly straight spines, and between these last two (4) patches of exceedingly minute and forked spines (Plate 14. fig. 22, *ay*). The remaining part of the tail is covered with the ordinary sort of spines which have just been mentioned in the large caudal and dorsal spines.

After the third of the movable spines has come out (*i. e.* after the fourth moult), one may find, in those specimens which are ready to moult again, seven segments under the skin, each of them with an appendage which looks very much like a future swimmerette (Plate 13. fig. 19, sp^3). The same thing may also be found in those speci-

mens which have already got four movable spines, and I have no doubt also in those with five and six spines. At first I thought that these segments and their appendages were indeed the future pleopods of the *Cypris*; but I found no traces of these *Nauplii* being otherwise prepared for the great change, indications which are invariably only to be found in those larvæ which are provided with six movable spines.

The underlying spines are therefore nothing but the future six large spines of the adult *Nauplius*.

How the pleopods develop in this latter stage before the change into the *Cypris* form takes place I do not know, having never been able to find a *Nauplius* in which they were clearly visible underneath; but judging from what we have seen in other Cirripedia, and from what we know about the development of the large spines, I have no doubt that they develop very much in the same way as these.

Although a certain segmentation under the *Nauplius*-skin cannot therefore be denied in the course of the development of the larva, no trace of this is visible as soon as the underlying skin becomes the external one, and the *Nauplius* of *Lepas fascicularis* never shows on the outside any segmentation in its tail. The movable spines simply mark the place where, later on, we find the segmented abdomen of the *Cypris*.

On our southern cruise, when we get into the regions of *Lepas australis*, I shall take up this subject again, and will make sure about this point, which is the only one of any consequence in the development of *Lepas fascicularis* which I have not quite been able to clear up.

The three appendages of the adult *Nauplius* have been, as I have said, very accurately described by Dohrn in his "*Archizoëa*," except that he has considered the third pair to be the second, and *vice versâ*.

The first antennæ are simple, with only one branch and six joints (Plate 12. fig. 15, *a*). On the first three joints there are no hairs, but on the second and third a few small spines may be seen, which have not been described in the southern larva. The fourth segment is the largest in both species; it has three long hairs on one side and one on the other. The last two segments are very small, the fourth with two, and the fifth with three long hairs.

During the metamorphosis of the *Nauplius* into the *Cypris* stage this is the only pair of appendages which remains; and in old *Nauplii* you may already find stages in which the sucker is being developed within. I have represented, in Plate 14. fig. 22ª, a stage in which a large number of nucleated cells is contained in the very much enlarged fourth segment, showing that something is going to be formed within (fig. 22ª, 4, *acet*). In the same figure traces of the two large joints of the *Cypris*-antenna may be seen, one of them being already visible in the first and second segment underneath the skin, and the second (the one that will have the sucker at the top) being formed inside the third and fourth. The last two segments have very much the same shape in the *Cypris* which they had in the *Nauplius*, only the number of hairs and setæ at the top differs considerably in the two stages.

I have never seen in these antennæ glandular ducts; but if I am right in supposing that the glands in the upper lip do not go into the stomach, a communication with them would be easily established when the great revolution takes place which changes the *Nauplius* into a *Cypris*.

The appendages of the second pair are the largest and are branched (Plate 12. fig. 15, *b*); the appendage has some setæ and a strong manducatory process (fig. 15, *r*) on the second segment; and on the third also there is a sort of manducatory organ with a very hairy surface, somewhat larger than the corresponding process figured by Dohrn in his *Archizoëa*. The branch which starts from this segment has in our case nine (not seven) segments. The fourth segment is covered on its inferior side with very strong hairs; the fifth is very long, and the sixth the shortest, with two long hairs at the top.

The appendage of the third pair (Plate 12. fig. 15, *c*) is also branched. It has on its second joint a conical process with a very strongly feathered short hair. Its branch, which starts from the third joint, consists of three segments, all of which have, as well as the fifth and sixth segment, long feathery hairs attached to them.

During these *Nauplius* stages the embryo has been rapidly growing, and has taken in plenty of food, consisting of small algæ which float at the surface. After the fifth moult it begins to accumulate materials for the pupa or *Cypris* stage, which it will now have to undergo, and during which no food is taken. Large masses of fat fill the space between the stomach and the carapace (Plate 14. fig. 22, *cl*), and make it appear quite opaque, while the developing *Cypris*-shell under the *Nauplius*-carapace gives to these old *Nauplii* a darker brownish colour.

Every thing is now ready for the next (sixth) metamorphosis, which diminishes the size of the larva in a most extraordinary way, and which is the most remarkable one which it has to undergo.

The carapace with its long spine, the tail and the caudal spine, the second and third pairs of appendages, and the large labrum are now all cast off, and the *Cypris* underneath is ready to swim about.

III. *The* Cypris *stage.*

The changes just mentioned take place evidently very suddenly, for I could never find a *Nauplius* which was just in the process of moulting, though I found plenty of empty and cast-off skins. After the metamorphosis the newly born *Cypris* takes to a different mode of life to that which was led by the *Nauplius*. The *Nauplii* come at night to the surface, but live in the daytime mostly in a depth of 60 fathoms, while the *Cyprides* are to be met with on the very surface, swimming in a lively way round the *Velellæ*, and trying to fix as soon as possible on dead individuals of these siphonophores. I should think that this *Cypris* stage lasts only a very short time; for in the same places where hundreds or thousands of *Nauplii* were caught we obtained only a few *free-swimming Cyprides*, but saw them in crowds on the young *Lepas* colonies, on

which they had settled wherever there was the smallest place left for them. The *Cypris* evidently attaches itself on the very first occasion, preferring for its future domicile *young* colonies of *Lepas* or *Velella*-shells on which there are as yet only *Cyprides* and no *Lepades* at all. This is the reason why the worst places for collecting them are old colonies of the barnacles, in which most of the specimens are about of the same age, and in which only here and there younger or just-fixed *Cyprides* may be found.

Lepas fascicularis is one of the barnacles which were studied by CLAUS when he worked out the last stages of the Lepadidæ; and I have no doubt he has seen and partially already described the same things which I am about to describe. In details, however (supposing the *L. fascicularis* of the Pacific to differ from the Atlantic one), there may be some differences.

Moreover we have the classical description which DARWIN* has given of the *Cypris* stage in *Lepas australis*, which from its large size (0·1 of an inch, about 3 millims.) is especially favourable for such a study, and which corresponds nearly in every detail with that of *Lepas fascicularis*. I shall therefore be very short in my description of the *Cypris*, as well as in that of the transition stage to the adult *Lepas*, in order not to repeat things at large which have already become the property of science; but I must give an account of the chief changes which occur in order to make my description of the *Lepas* development complete.

The size of the *Cyprides* is variable; some of them have a length of 1·3 millim. and a width of 0·7 millim.; but some specimens may be found to be a little larger and some a little smaller.

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The yellowish and rather transparent shell has an oval shape, but is pointed at the posterior end (Plate 15. fig. 24). When alive the whole animal's body is so much expanded by the cells of adipose matter, that scarcely any thing but the antennæ, the eye, and the setæ of the feet can be seen. But after having been put into absolute alcohol and then made transparent every thing comes out very well, and one gets, even without dissection, a good idea of its anatomical peculiarities.

The valves of the shell are kept chiefly together by a large *musculus adductor* (fig. 24, *ma*), which partly covers the parts of the mouth if you look at the entire shell. The muscle occupies a very large spherical place of attachment, and keeps the valves very strongly together.

The other muscles are those which run from the dorsal portion of the shell to the origin of the antennæ, and those which attach the upper portion of the body, and especially the head, to the upper portion of the shell. Two small muscles move continually the capsules which include the large compound eyes (fig. 24, *m*).

The Appendages.—Between the antennæ there are still remains of the two feelers which I saw when dissecting the pupa, but which I never could observe *in situ*. The *antennæ* (Plate 15. fig. 24, *a*, and fig. 27) are very large and powerful organs. How they originated in the first appendages of the *Nauplius* has been already described. In

* *Loc. cit.* ii. p. 14.

the free-swimming *Cypris* they are to be seen in connexion with a gland (fig. 24, gl^1), which may be easily seen on the ventral side of the stomach, often filled with granular secretions, which make it appear dark when seen by transmitted light. The duct of this gland runs up through the first and second joints of the antennæ and opens in the centre of the sucker (fig. 27, *dgl* and *acet*).

The antenna itself consists of four joints, not of three, as was formerly supposed by Darwin, who very likely had not seen the minute third one generally hidden by the sucker. Claus, however, and very likely Pagenstecher, have already described the right number. The first joint attaches with a forked base to the muscles of the body, and has a strong curved spine. The second joint is nearly as long as the first. Its largest muscles run all towards the sucker, which is attached by a short peduncle to its exterior side. The diameter of the sucker is 0·1 millim. It has a depression in the middle to receive the duct of the gland, and round this depression a wall of chitinous substance, on which seven large spines, two small spines, and four setæ are attached. Another seta is found below the sucker on the second joint, in the same place where in the *Nauplius* we saw a feathered hair. The third joint, almost hidden by the sucker, is very small; and the fourth only somewhat larger, but distinguished by four setæ and two olfactory hairs, between which there is a broad paddle-shaped appendage which I cannot well classify (fig. 27, *u*). Under an immersion-power you see a double contour line running up into it, but no hairs nor appendages of any kind at the top. Darwin has observed the same number of setæ, hairs, and also this peculiar appendage in the pupa of *Lepas australis**.

The second and third appendages of the *Nauplius* stages are entirely lost, and so is the large labrum; only a small helmet-like prominent organ is to be seen where formerly we found such a huge appendage, the two lateral glands of which have now very likely been converted into shell-glands. There are three parts of the mouth besides the upper lip (fig. 32, *a*, *b*, *c*), all very rudimentary. I have been unable to separate them quite satisfactorily, though I have tried ever so many times to get at them with fine needles. Claus, however, has succeeded in doing so, and has shown, when comparing the whole of the *Cypris* stage with the Copepods, that these parts correspond to the maxillæ and maxillipeds of these Entomostraca.

I think there is no reason to doubt the disappearance of the third appendages; for I have looked very carefully whether any remains of them could be found, but did not succeed, and I think that if any thing developed itself at all in these large appendages it would be easily seen. The parts of the mouth, it is true, are very small; but with the exception of the labrum, which is easily found, they are all new formations.

There are six pairs of branched natatory feet, five of which have been compared by Claus to the natatory feet of the Copepods, and the last pair to their genital appendages. These feet are adorned with a short seta, which is directed upwards, on the front of the last segment, and with long, very densely feathered setæ at the end.

* Darwin, *loc. cit.* tab. 30. fig. 8.

They offer nothing at all peculiar, and consist of three joints, the first of which is the one from which the two branches start. Each of these consists accordingly of two joints.

Between these natatory feet slender chitinous lamellæ are seen running up on both sides of the abdomen (fig. 24, *la*), which separate the spaces from each other, in which after a short while the large cirri of the *Lepas* will develop, after the temporary feet of the *Cypris* have been deprived of the plastic substance which they contain. This shows out extremely well in one of my preparations, a *Cypris* which has just begun to give the first signs of metamorphosis; also in fig. 25 this is still sufficiently visible.

The two-jointed appendages of the tail are mostly turned upwards, and have setæ on their last joints, similar to those on the natatory feet.

The Organs of Sense.—Between the antennæ, and a little behind them, two small protuberances might be observed, which CLAUS calls the "Stirnhöcker," and which are very likely the remains of the lateral horns. No function seems, however, to be assigned to them now, as they have neither terminating glands nor any appendages which might be organs of touch.

As sense-organs we have in the first place to claim the two olfactory hairs on the last joint of the antennæ, and as organs of touch the setæ and the peculiar elongate and flattened appendage which has been represented in fig. 27, *u*; also the setæ on the sucker and the one on the second segment are very likely used as such.

The nervous system is represented by two large ganglia (Plate 13. fig. 21, *cer*), which are of an oval shape, and very likely united by a nervous bridge, which in our figure has been given with some doubt. These ganglia, in which nucleated cells may be observed, send large nerves to the base of the large compound eye, which consists of a black pigment body, eight to ten lenses and their cornea. The eye is at the bottom of a large capsule, very likely containing fluid, and attached to one of the valves by small muscles which enable it to move in different directions. Besides these large eyes we still find the *Nauplius* eye in the same place in which it was before, between the two antennæ, a little above their points of attachment.

Organs of Digestion and Glands.—The parts of the mouth which have been already described lead through a short œsophagus into the stomach, on both sides of which I saw, when dissecting the pupa, small glands, which seem to lead into the œsophagus as they do in the full-grown *Lepas*.

The stomach is now rather collapsed, never distended by food like that of the *Nauplius* stage. It passes into an intestine, which is much longer than that of the latter, and ends most likely with an anus at the base of the last pair of natatory feet. I have, however, not been able to see this opening, nor could I find as yet a trace of the excretory cæca, which in the adult *Lepas* terminate on both sides of the rectum.

Besides the œsophageal glands there are the cement-glands, which lead into the antennæ and which have been traced from their first origin in the upper lip and described with the antennæ. Very conspicuous as lying under the shell in the dorsal

part of the pupa is the large shell-gland (fig. 24, *gl*^{2}), the function of which is to supply first the materials for the five primitive valves of the shell, and then the shells themselves, which, according to Claus's and my own observations, are formed after those small valves and separately from them, so that the former always remain in the shell and are easily recognized by their peculiar cellular structure.

Traces of an ovary have also been found in the pupa stage, and figured as seen under a low power in fig. 28.

IV. *The metamorphosis of the* Cypris *into the* Lepas.

The pupæ swarm round the dead *Velellæ*, and settle by means of their hooks and suckers as soon as they find a suitable place. None of the metamorphoses, therefore, are easier to study than these, as one young colony caught during the season of their development shows all the stages—the pupa which has just settled and not yet changed its form (Plate 15. fig. 24), the same after its head had grown out and when its *Cypris*-shell and natatory feet are just going to be cast off (fig. 25), and the perfect young *Lepas* (fig. 26). Still what happens within is more difficult to observe, as the transparency, which hitherto guided us in our researches, is less and less to be found as the pupa develops.

The growing out of the head and the appearance of the feet in that part of the abdomen which in the *Cypris* (fig. 24, *la*) is divided by ridges and chitinous lamellæ, is the first thing that happens; and now one may also see very faint traces of the cellular tissue of the primitive valves. The eyes, however, are still in their position, and the *Cypris*-shell still covers the body. The next stage (fig. 25) is the loosening of the *Cypris*-shell and of the moulted natatory feet, which in fig. 25 may be seen just coming off. Underneath six pairs of cirri (*p*) may be seen, which still differ from those of the adult *Lepas* in being less segmented and not so hairy. The three primordial valves are now fully formed, and are very striking from their regular network of cellular tissue. The eyes of the *Cypris* stage have already lost their proper position, but may still be seen as black pigment-spots, which are about to be absorbed; they look like pictures which have lost their frames, and will soon entirely disappear. The upper lip is now very prominent, and the organs of digestion are shining through the valves in formation.

From the two large glands underneath the mouth, in front of the stomach, ducts filled with granular secretion may be seen going down to the antennæ (fig. 25, *a*), which by-and-by have to form a gelatinous ball which finally absorbs the fragment of *Velella*.

In this stage the upper portion is 1 millim. long, the grown-out head having a length of 0·7 millim. It now throws off entirely all the larval remains; the valves of the *Cypris*-shell drop with the old feet and caudal appendages, and round the primordial valves, which indicated already the position of the larger ones, a more solid skeleton

is formed. The cirri have acquired a greater number of segments (fig. 26); and the young *Lepas*, which has now a length of 4 millims., is complete.

Conclusion.

The chief object of this paper has been to give a complete history of a *Lepas* development which hitherto had never been worked out. The first and the last stages were known in some species, and in another species the intermediate pelagic stages had been described by Dohrn; but it was not even known to what family of Cirripedia these *Nauplii* belonged. This is quite natural, as all the work for such a complete development must be done under conditions which scarcely ever had been realized before this ship left the shores of England.

There are only few points in this paper which will enlarge our ideas about the morphological relations of Cirripedia very much, in so far as each of the larval stages were known to exist before; but it settles the question to which of the Cirripedia the large pelagic *Nauplii* belong, and it gives further details about their intimate structure. It also gives certain indications which allow us to say, almost to a certainty, to which of the *Lepas* species the larvæ belong which Dohrn got in the south, and which have been taken by ourselves to the south of Australia; but it likewise gives evidence that there are no traces of a *Zoëa* stage in the course of the *Lepas* development. The *Nauplii* are very highly organized, but there are no essential differences between them and the other embryonic forms which we have been accustomed to call *Nauplii*. The name of *Archizoëa* might, I think, be left to keep up the remembrance of Dohrn's discovery of the interesting *Lepas* larvæ; but speaking of the Lepadidæ in general, I think it would only confuse matters if it were said that they pass through an *Archizoëa* stage. This would imply that the later *Nauplius* stages of *Lepas* have a different morphological value from those of *Balanus* or other genera, which I think they have not.

Description of the Plates.

PLATE 10.

Fig. 1. Development of the ovarium (*m*): *n*, the ovum nearly filled with yelk, still showing the germinal spot.

Fig. 2. Ovarian tube with young ova in the beginning of their development.

Fig. 3. Ovarian tube with nearly mature ova. Among them some undeveloped cells (*oi*), perhaps the mother cells of the ova.

Fig. 4. Complete ovum, before the beginning of the segmentation, taken from the ovisac. The germinal vesicle is not visible. Nat. size, 0·26 millim.

Figs. 5 & 6. First stages of segmentation. Four blastodermic cells have formed themselves.

Fig. 7. Segmentation of the yelk goes on, but is not clearly visible. More blastodermic

cells in the interior. On the right side the yelk gives way at the place where afterwards there will be a groove between the appendages: *y*, blastodermic cell; *x*, yelk-globules.

Fig. 8. The blastoderm has spread all over the ovum and enclosed the yelk. Reflected light.

Fig. 9 *a*. Front view; fig. 9 *b*, side view. First formation of the three pairs of appendages (*a*, *b*, *c*).

Fig. 10. The embryo in its thinner and enlarged (? blastodermic) cuticle, length 0·28 millim.: *a*, *b*, *c*, the three pairs of appendages; *la*, labrum.

Fig. 11. The *Nauplius* having just come out. Dorsal view: *a*, *b*, *c*, the three appendages; *cp*, the lateral horns; *la*, labrum; *oes*, œsophagus; *c*, cauda; *prc*, processus caudalis, or the spine attached to the tail's posterior side. These two are invaginated and enveloped by a very thin cuticle, as also are the ends of the lateral horns (figs. 11 *a* & 11 *b*). Natural size: length 0·35 millim.

Fig. 12. An adult *Nauplius* (*Archizoëa*, Dohrn) seen from the side. × 12 nat. size.

All the figures, with the exception of fig. 12, were drawn under a high power. (Hartnack $\frac{1}{7}$ or $\frac{1}{8}$.)

PLATE 11.

Fig. 13. *Nauplius* after the first moult. Drawn from specimens kept in globes as well as from those caught on the surface. *a*, *b*, *c*, the three appendages; *cp*, cornua parietalia; *la*, labrum; *oes*, œsophagus; *sp*, the first one of the large spines on the tail; *ac*, the caudal spine; *x*, feelers; *z*, spines of the carapace. Natural size of this embryo:—

Length of the whole animal	0·61 millim.
Length of front of embryo	0·17 „
Length of cornua parietalia	0·26 „
Length of carapace	0·19 „
Length of tail	0·42 „

Fig. 14. *Nauplius* after the second moult. From the surface of the Pacific. Letters the same as in the last figure, except:—*cer*, first formation of the ganglia; *coe*, glandular bodies; *pr*, processes of the carapace, into which the unicellular glands send their ducts; *ad*, dorsal spine.

PLATE 12.

Fig. 15. *Nauplius* (*Archizoëa*, Dohrn) after the fifth moult. From the surface. The tail with its large dorsal spine has been bent over a little to the side to show the end of the intestine and the glands; also the labrum has been turned over a little to show the mouth and the narrow channel by which it is in communication with the œsophagus. The muscles in the tail and the caudal and dorsal spines have grown, and, not being able to stretch out, are taking

turns like a corkscrew. In the tail there is a gland (*gl*) which seems to have its opening into the lower part of the stomach. The epithelium in the upper part of the stomach is a little diagrammatic, not being in reality quite so regular, and the cells being more darkened by granules than they are in the figure.

Letters the same as in the last figures, except:—sp^3, immovable large spine; *pi*, pigment-spot, just above the entrance of the stomach; *as*, anus; *r*, processus mandibularis. Natural size:—

Diameter of carapace	1·0 millim.
Length of tail	4·0 millims.
Length of processus caudalis	6·0 „

Fig. 15ª. Enlarged view of the manducatory process of the second antenna. High power.

PLATE 13.

Fig. 16. One of the processes on the carapace of the *Archizoëa* (later *Nauplius* stage), showing the glands terminating in them and the nerves in connexion with these glands. Observed on a living specimen under very high power (Hartnack no. 10). *gl*, the large and main gland opening into *pr*, the process of the carapace; *m*, outer margin of the carapace; *y*, a sense-hair on the same; *n*, varicose nerve running up to it; *n*, nervous stem sending a branch to the bottom of the gland, *gl*; *c*, a ganglionic cell.

Fig. 17. One of the lateral horns seen from above. H. $\frac{1}{4}$. From a living specimen. *gl*, the large glands, the bottoms of which are fastened by fibres of (?) connective-tissue or muscles; *pr*, processes in connexion with smaller glands; *q*, ring for the attachment of the muscles; *ch*, inverted portion of chitinous cuticula; *y*, a sense-hair; *z*, hairs at the top of the lateral horn, very likely in communication with a nerve, which, however, could not be found.

Fig. 18. Eye of a young *Nauplius* after its fifth moult, and on both sides the feelers with their nerves. Underneath the two ganglia. Very high power. H. $\frac{1}{10}$. *x*, feeler; *n*, varicose nerve; *cer*, ganglia; between the eye and the feelers a granular (? nervous) substance.

Fig. 19. Portion of the tail of a *Nauplius* after its fourth moult. Only three large flexible spines have as yet come out (*sp*), but seven spines (sp^2) may be seen ready to come out under the skin. The seventh is the future large immovable spine. High power.

Fig. 20. The tail of an adult *Nauplius* (last *Archizoëa* stage) showing the muscles going to the movable spines. High power.

Fig. 21. The ganglia (*cer*) of the *Cypris* stage; the nerve going to one of the compound eyes (*oc*), and the capsule round the latter. High power. The connecting dotted line (*hy*) between the two ganglia indicates that it is a hypothetical one, not observed.

PLATE 14.

Fig. 22. An adult *Nauplius* after its fifth moult (last *Archizoëa* stage). The labrum is in its ordinary position. All the appendages have been removed, in order to show the glandular system inside the carapace and the masses of adipose pigment accumulating there. The latter are only shown on one side in order not to confuse the drawing. From the surface. H. ½. *ac*, caudal spine; *ad*, large dorsal spine; *ay*, small forked hooks on the middle line of the tail (fig. 22, *ay*, the same seen under very high power); *coe*, cæca in the upper lip leading into the stomach; *cl*, adipose body (fat-cells); *cp*, lateral horns; *dr*, glands in the interior of the carapace; *gl*, glands terminating in the processes of the carapace; *nc*, nervous cell; *n*, nerves; *o*, first formation of the lateral eye, which very soon will present the same aspect as those drawn in fig. 23, *o*; *oes*, œsophagus; *pr*, processes of the carapace, with an opening of the gland at the top; sp^1, movable spines; sp^2, immovable spine; *x*, feelers. Natural size:—

Diameter of the carapace	2 millims.
Length of the tail	8 „
Length of the caudal spine . . .	12 „

Fig. 22^a. First antennæ of an adult *Nauplius* near its last moulting into the *Cypris* stage. 1–6, the joints; *a*–*e*, the underlying joints of the *Cypris* antenna; *acet*, the cells which build up the sucker.

Fig. 23. Anterior part of the *Nauplius*, last *Archizoëa* stage of a Cirriped from the surface of the Antarctic sea (? *Lepas australis*, described by Dohrn as *Archizoëa gigas*), in order to show the processes into which the glands terminate all over the carapace, and the state of the lateral eyes before the moulting for the *Cypris* stage takes place. From a preparation in Canada balsam. H. ½. *la*, labrum; *gl*, glandular system inside the carapace; *pr*, processes; *cp*, lateral horns; *y*, vesicular connective-tissues, patches of which are to be found in the glandular substance of the carapace; *x*, the feelers; *o*, the two compound lateral eyes of the *Cypris* stage into which this *Nauplius* was preparing to moult. Natural size:—

Length of carapace	2·0 millims.
Width of carapace	1·50 millim.

PLATE 15.

Fig. 24. Free-swimming *Cypris* stage (after the sixth moult), from the sea-surface. Antennæ and feet retracted into the shell. Partly from living specimens, partly from Canada-balsam preparations. H. ½. *a*, the antennæ, with the sucker; *m*, different muscles; *ma*, musculus adductor; gl^1, gland leading into the antennæ; gl^2, gland of the shell (visible in nearly all prepared speci-

mens); *dgl*, duct of the gl^1, leading into the sucker of the antenna; *oc*, the large compound eye in its capsule and the muscles attached to the latter, by which its continual vibrating movement is effected; *pl*, the abdominal feet; *c*, the caudal processes. Natural size:—

Length	1·30 millim.
Width	0·70 „
Diameter of eye	0·09 „
Diameter of lenses	0·02 „
Diameter of sucker	0·10 „

Fig. 25. The *Cypris* stage, having fastened itself by means of a sucker on the "sail" of a dead *Velella*, in the act of throwing off its *Cypris*-shell and feet, of losing the compound eyes, and of forming the primordial valves. The end which in fig. 24 is the upper one is here the lower, from which the "plastic" parts of the body have retired towards the top. The animal has been taken off from the *Velella*, and the drawing has for the most part been made from a Canada-balsam preparation. H. $\frac{1}{7}$.

I. *The young* Lepas.

a. The antennæ, with the sucker.
ped. The pedunculus of the young *Lepas*.
o. The mouth.
p. The newly formed feet (cirri).
ta^1, ta^2, ta^3. The primordial valves.

II. *The Remains of the* Cypris *which are thrown off*.

pl. The dropping feet of the *Cypris* stage.
c. The caudal appendage of the *Cypris* stage.
oc. The compound eyes, already dropped and going to be absorbed.
v. The valves of the shell.

Natural size:—

Length of upper portion of the young *Lepas* (not counting the *Cypris*-shell)	1·0 millim.
Length of lower portion (formerly the head of the *Cypris*)	0·7 „
Height of ta^1	0·7 „
Length of ta^2	0·2 „
Height of ta^3	0·8 „

Fig. 26. Young *Lepas* fixed on the sail of a dead *Velella* (*Ve*). Low power. H. $\frac{1}{4}$. *a*, antennæ, with sucker sticking to the *Velella*-sail; *ped*, pedunculus; *ca*, carina; ta^1, ta^2, primordial valves. The reticulated structure is here only

indicated by dots, as coming out well only when a higher power is used. Natural size:—

Length of pedunculus	1·0 millim.
Length of upper portion	3·0 millims.
Total length	4·0 „
Height of ta^1	0·4 millim.
Length of ta^2	0·3 „

Fig. 27. The antenna of the *Cypris* stage. 1, 2, 3, 4, the four joints; *acet*, the sucker; *sp*, spine at the base of the joint which is attached to the body; *dgl*, duct of the gland; *m*, muscles; *set*, setæ; *cs*, olfactory hairs; *u*, flat, doubtful appendage, enlarged in fig. 27, *u*.

Fig. 28. First formation of the ovary in the *Cypris* stage, got by dissecting the animal when alive.

Fig. 29. First maxilla of the adult *Lepas*.

Fig. 30. The mandibles of an adult *Lepas*. *a*, the right mandible, with five teeth; *b*, the left mandible, with six teeth.

Fig. 31. Half of the labium (second maxilla) of an adult *Lepas*. H. $\frac{1}{4}$.

Fig. 32. The organs of the mouth, as seen *in situ* in a dissected *Cypris*. As I did not succeed in separating them well, they may not have come out quite accurately. High power. *a*, mandible; *b*, first maxilla; *c*, second maxilla.

[Note.—The author of this paper, a young naturalist of the highest promise, died on board the 'Challenger' on the voyage from the Hawaiian Islands to Tahiti. In correcting this his last scientific paper for the press I have made as few changes as possible, only altering the arrangement here and there to make the English run more smoothly; and, in memory of his industry and enthusiasm, I have allowed several passages to stand referring to his hopeful anticipations for the future.—C. Wyville Thomson.]

VI. *On Rolling-Friction.* *By Professor* Osborne Reynolds, *of Owens College, Manchester.* *Communicated by Professor* B. Stewart, *F.R.S.*

Received May 24,—Read June 17, 1875.

Introduction.

Although the motion of wheels and rollers over a smooth plane is attended with much less resistance or friction than the sliding of one flat surface over another, however smooth, yet practically it has been found impossible to get rid of resistance altogether. Coulomb made some experiments on the resistance which wooden rollers meet with when rolling on a wooden plane, from which experiments he deduced certain laws connecting this resistance with the size of the rollers and the force with which they are pressed on to the plane. These laws have been verified and extended to other materials by Navier and Morin, and are now set forth in many mechanical treatises as "*the laws of resistance to rolling.*" It does not appear, however, that any systematic investigation of this resistance has ever been undertaken or any attempts made to explain its nature. When hard surfaces are used it is very small, and it has doubtless been attributed to the inaccuracies of the surfaces and to a certain amount of crushing which takes place under the roller. On closer examination, however, it appears that these causes, although they doubtless explain a great part of the resistance which occurs in ordinary practice, are not sufficient to explain the resistance altogether; and that, if they could be removed, there would still be a definite resistance depending on the size and weight of the roller and on the nature of the material of which it and the plane are composed. If it were not so, a perfectly true roller when rolling on a perfectly true surface ought to experience no resistance, however soft the roller and the plane might be, provided both were made of perfectly elastic material so that the one did not crush the other; and we might expect, although these conditions are not absolutely fulfilled, that a roller of iron would roll as easily on a surface of india-rubber as on one of iron, or that an india-rubber roller would experience no more resistance than one of iron when rolling on a true plane. Such, however, is not the case. The resistance with india-rubber is very considerable; my experiments show it to be ten times as great as with iron. I am not aware that this fact has been previously recognized; and that it has often been overlooked is proved by the numerous attempts which have been made to use india-rubber tires for wheels, the invariable failure of which may, I think, in the absence of any other assigned cause, be fairly attributed to the excessive resistance which attends their use. Another fact which I do not think has been hitherto noticed, but of which I have had ample evidence, and which clearly shows the existence of some hitherto unexplained

cause of resistance to rolling, is the tendency which a roller has to oscillate about any position in which it may be placed on a flat surface.

However true and hard the roller and the surface may be, if the roller is but slightly disturbed it will not move continuously in one direction until it gradually comes to rest, but it will oscillate backwards and forwards through a greater or less angle, depending on the softness of the material. These oscillations are not due to the roller having settled into a hollow. This is strongly implied by the fact that the more care is taken to make the surfaces true and smooth the more regular and apparent do the oscillations become. But even if this is not a sufficient proof—if it is impossible to suppose that an iron roller on an iron plane can be made so true that when the one is resting on the other it will not be able to find some minute irregularities or hollows in which to settle—still we must be convinced when we find the same phenomenon existing when india-rubber is substituted for iron, and in such a marked degree that no irregularities there may be in the surface produce any effect upon it, much less serve to account for it.

These phenomena, with others, have led me to conclude that there is a definite cause for the resistance to rolling besides the mere crushing of the surface or accidental irregularities of shape, a cause which is connected with the softness of the material as well as with the size and weight of the roller.

Such a force, if its existence be admitted, must either be considered as exhibiting some hitherto unrecognized action of matter on matter, or must be supposed to arise in some intelligible manner from the known actions. The latter is the most natural supposition; and it is *my object in this paper to show that this force arises from what is ordinarily known as friction.* It is to imply this connexion that I have gone back to the name *Rolling-Friction* in place of the more general title *resistance to rolling* ("résistance au roulement"), which COULOMB and subsequent writers have chosen avowedly because they did not wish to imply such a connexion.

The assumption that this force is due to friction necessarily implies that there is slipping between the roller and the plane at the point of contact; and on the other hand, if it can be shown that there is slipping, it follows as a natural consequence that there must be friction or resistance to rolling. Therefore the question as to whether the resistance to rolling is due to friction reduces itself into a question as to whether there is any evidence of slipping between the roller and the surface on which it rolls.

My attention was first called* to the possibility of such slipping while considering a phenomenon in the action of endless belts when used to transmit rotary motion from one pulley to another, namely that it is impossible to make the belt tight enough entirely to prevent slipping and cause the surfaces of the two pulleys to move with identically the same velocity. It appears that this slipping is due to the elasticity of the belt, and, since all material is more or less elastic, cannot altogether be prevented.

* The Engineer, November 27, 1874.

This becomes apparent when we consider that of the two parts of the belt which stretch from pulley to pulley the one is tighter and hence more stretched than the other, that is, when the belt is transmitting power. For that side which is most stretched, and consequently thinner, will have to move faster than the slacker side in order to prevent the belt accumulating at one pulley; and the speed of the driving-pulley will be equal to that of the tight side of the belt, while the speed of the following pulley will be equal to that of the slack side. This difference of speed requires that the belt shall slip over the pulleys; and this slipping takes place by the expansion and contraction of the belt on the pulleys as it passes from the tight side to the slack side, and *vice versâ*. With leather belts this slipping is very small; but with soft india-rubber it becomes so great as practically to bar the use of this material for driving-belts.

The recognition of this slipping at once suggested to me that there must be an analogous slipping when a hard roller rolls on a soft surface, or when an india-rubber wheel rolls on a hard surface. A single experiment was sufficient to prove that such was the case—an iron roller rolled through something like three quarters of an inch less in a yard when rolling on india-rubber than when rolling on wood or iron.

Having made this discovery, I proceeded to investigate the subject, and have obtained what I think to be satisfactory evidence that, whatever may be the material of which the plane and the roller are composed, the deformation at the point of contact always causes slipping, although, owing to the hardness of the materials, it may be far too small to be measured.

In the following paper I shall first show that the deformation at the point of contact caused by the weight of the roller must affect the distance rolled through, that it must cause slipping, and that this slipping will be attended with friction. I shall then show that the friction will itself considerably modify the deformation which would otherwise take place, and endeavour to trace the exact nature of the actual deformation. The result of my experiments will then be given, together with the description of certain other causes of rolling-friction which appear under certain circumstances to exist. In conclusion, I shall indicate the direction in which I hope to continue the investigation, consider its bearing on the laws discovered by COULOMB, and discuss certain phenomena connected with the wear of railway-wheels which have been hitherto unexplained, and which serve to illustrate the importance of the subject.

The Distance Rolled through.

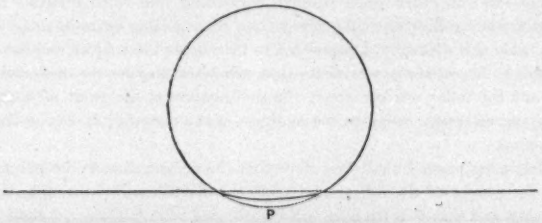
If a perfectly hard cylinder rolled on a perfectly hard plane and there were no slipping, then the distance which the cylinder would pass over in one revolution would be exactly equal to its circumference; but if, from the weight of the cylinder or any cause, the length of the surface either of the cylinder or the plane underwent an alteration near the point of contact, then the distance traversed in one revolution would not be equal to the natural length of the circumference. For example, suppose that an iron cylinder is rolling on a surface of india-rubber across which lines have been drawn at

intervals of ·01 of an inch, and suppose that as the cylinder rolls across these lines the surface of the india-rubber extends so that the intervals become equal to ·011 of an inch, closing again after the cylinder is past, then the cylinder will measure its circumference (so to speak) on the extended plane, and the actual distance rolled through when measured on the contracted surface will be one tenth less than the circumference. In the same way there would be an alteration in the distance rolled through if the surface of the roller extended or if either of the surfaces contracted.

In the subsequent remarks I shall call the distance which the roller would roll through if there were no extension or contraction its geometrical distance.

Since no material is perfectly hard, when a heavy roller rests on a surface the weight of the roller will cause it to indent the surface to a greater or less extent according to the softness of the latter; and in the same way the surface of the cylinder will be flattened at the point of contact in the manner shown in fig. 1.

Fig. 1.



This indentation and flattening will alter the lengths of the surfaces at the point of contact, and will therefore affect the progress of the roller. When a body of any shape is compressed in one direction it extends in the other directions; hence the weight of the roller resting on the plane will, by compressing the material of the plane in a vertical direction, cause it to extend laterally at the point of contact, and thus the length of the surface which the cylinder actually rolls over would be greater than the length measured on the undisturbed plane. From this cause, therefore, the cylinder would roll through less than its geometrical distance.

On the other hand, the surface of the roller would also be extended (squeezed out) in a similar manner by the pressure of the plane at the point of contact; and hence the surface of the roller would be greater than its natural length, and this would cause the roller to roll through more than its geometrical distance.

To a certain extent, therefore, the expansion of the surface of the roller would counteract the expansion of the plane; and if the two were of the same material, then the one of these extensions would, if nothing interfered to prevent it, exactly counteract the other. But if the one was harder than the other, then the effect is that one would be least. Thus an iron cylinder rolling on an india-rubber plane would roll through

less than its geometrical distance; whereas, inversely, an india-rubber roller on an iron plane would roll through *more than* its geometrical distance.

These things actually take place. But there is, besides softness, another circumstance not hitherto mentioned which affects the lateral extension of the surface when compressed by the roller, viz. *the shape of the surface*.

A little consideration will be sufficient to show that a curved indent in a flat surface will have a greater effect to extend the surface than a flat indent on a rounded surface. In the case of the rounded surface it will be seen that the effect of vertical compression to a certain extent counteracts the effect of lateral expansion; whereas in the case of the flat surface these things are reversed, and the effort of the surrounding material to uphold that which is depressed will increase the lateral expansion.

From this cause, therefore, even if the cylinder and the plane were made of the same material, there would still be a difference in the lateral extension of the surfaces at the point of contact depending on the smallness of the diameter of the cylinder, and this difference would still cause the cylinder to roll through less than its geometrical distance.

If, instead of on a plane, the one cylinder rolled on another parallel cylinder under a force tending towards the centre, then, if the two cylinders were of the same material and their diameters were equal, they would roll through their geometrical distance; but if the one was larger than the other, the largest would be most retarded.

It appears, therefore, that there are two independent causes which affect the progress of a roller on a plane—the relative softness of the materials and the diameter of the roller. Of these the curvature of the roller always acts to retard its progress; while the other (the relative softness) to retard or to accelerate according as the plane is softer than the cylinder, or *vice versâ*. These two causes will therefore act in conjunction or in opposition, according to whether the roller is harder or softer than the plane. In the former case the roller will be retarded, whereas in the latter it will depend on the relation between the relative softness and the diameter of the cylinder whether its progress is greater than, less than, or equal to its geometrical progress. Thus an iron roller on an india-rubber plane will make less than its geometrical progress; while an india-rubber cylinder on an iron plane will make more than, less than, or exactly its geometrical progress, according to the relation between its diameter and softness, or, what comes to the same thing, its weight, which conclusions are borne out by experiment.

The Slipping.

The lateral extension of the material, and the effect this has on the progress of the roller, causes slipping between the surface of the roller and that of the plane; for the surface of the roller, owing to the indentation and flattening, really touches the surface of the plane over an area of some extent; and the pressure between these surfaces, which is greatest towards the middle of the area in which they touch, will shade off to

nothing at the edges. Thus deformation is allowed to go on between the surfaces after they have come in contact, and is performed by the slipping of the one over the other.

The Friction.

The slipping is performed against friction, and therefore gives rise to resistance to the motion of the roller.

This resistance will obviously be proportional to the work spent in overcoming the friction between the surfaces during a certain extent of motion; and at first sight it appears as if this would be proportional to the coefficient of friction between these surfaces. When I first commenced this investigation I was under the impression that such would be the case, and that by oiling the surfaces the resistance to rolling might be considerably reduced. Finding by experiment, however, that this was not the case, that although in certain cases the effect of oiling or blackleading the surfaces does reduce the resistance to rolling, yet this reduction is never great, and in some cases the effect appears to be reversed, it occurred to me that the friction would itself modify the deformation which would otherwise take place after contact had commenced, and by preventing slipping might diminish the work that would otherwise have been spent.

The Deformation.

The action of friction to prevent the deformation at any point of the surfaces in contact will obviously depend on two things—the magnitude of the friction, and the force tending to slide the one surface over the other. Now if P (fig. 1) be the point of greatest pressure, the possible friction will gradually diminish with the pressure as the distance from P increases; whereas we may assume that the tendency of the one surface to slip over the other will be nothing at P, and will gradually increase with the distance; so that for a certain distance the friction may be sufficient to prevent slipping altogether, but beyond this distance slipping will go on in an increasing ratio.

The effect of oiling the surface would therefore be to diminish the region of no slipping, and increase the area over which slipping goes on as well as the extent of slipping at each point. These effects would to a certain extent counteract the advantage gained by the reduced coefficient of friction; and it may well be conceived that under certain circumstances they would overbalance it, and that the oil would actually increase the resistance.

The effect which friction has upon the deformation beneath the roller, as well as the general nature of this deformation, will be rendered clearer by examining the effect of friction under circumstances of a less complicated nature than those of rolling.

A Soft Bar between Hard Plates.

Let fig. 2 represent the end or a section of a long rectangular bar of india-rubber, or any elastic material, placed between two flat plates. Suppose these plates to approach

each other, compressing the india-rubber, which will extend laterally. Now if there were no friction between the rubber and the plates, then the surfaces in contact with the plates would extend in the same proportion as the rest of the bar, and the section would preserve its rectilinear form, as shown in fig. 3.

Fig. 2.

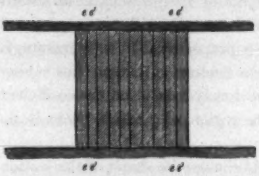


Fig. 3.

With friction, however, the case would be different. The friction would prevent the surface of the india-rubber expanding laterally to the same extent as the rest of the bar, and the section would lose its rectilinear form and bulge out in the middle, as shown in figs. 4 and 5.

Fig. 4.

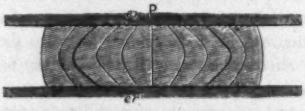


Fig. 5.

If we imagine the section of the bar to have been marked with a series of lines (ee') initially vertical and at equal intervals apart, these lines will when the bar is compressed assume the form shown in the figures.

If there were no friction, then, as shown in fig. 3, the ends of these lines would still be equidistant after compression; but with friction the intervals will not be all equal, but will vary according to their distance from P, the middle of the section. Up to a certain distance (er) the friction will be sufficient to prevent slipping; and hence up to this point the ends of the lines will preserve their original distance. From this point (er), however, slipping will commence and will go on increasing to the edge of the surface. From this point, therefore, the distance between the ends of the lines will continually increase.

With regard to the distribution of the pressure between the india-rubber and the plates:—Without friction this will obviously be uniform over the whole surface. Friction, however, will not only increase the mean intensity of the pressure, but will also alter its distribution, causing it to be greatest at P and gradually diminish towards the edge.

The inclination of the ends of the lines ee' is caused by, and may be taken to repre-

sent, the intensity of the friction at the surface. As long as there is slipping the friction will be proportional to the pressure. Therefore from the edge of the surface to *er* the inclination will continually increase; and it will be greatest at *er*, for from this point inwards the tendency of the india-rubber to slip will obviously diminish until it vanishes at P.

The distance of er *from* P *will not depend on the degree of compression*, at all events so long as this is but small, for the tendency to extend laterally will be proportional to the intensity of the pressure; and since the friction is proportional to the pressure, it will increase at all points in the same ratio as the forces tending to extend the rubber laterally. The distance of *er* from P will, however, obviously depend on the coefficient of friction. The greater this is the greater will be the region over which there is no slipping.

By blackleading the india-rubber, therefore, we should change the shape of the section from that shown in fig. 4 to that shown in fig. 5, in which all the ends of the lines from *er* to the circumference are less inclined than the corresponding lines in fig. 4, and the intervals between them greater, showing that not only is the friction less and the area over which it acts greater, but that each point has also to slip through a greater distance.

It is difficult to say how far these two latter effects will compensate for the former. We may, however, show that there must be some value of the coefficient of friction for which the work spent in overcoming the friction will be a maximum; for when the coefficient was very great *er* would be at the circumference and there would be no slipping, and hence no work spent in friction; whereas if the coefficient were zero, *er* would be at P, and there would be no friction and consequently no work lost in overcoming it. Therefore the work spent in friction, which is a function of the coefficient of friction, is zero for two values of the variable; and since it is positive for all intermediate values, it must pass through a maximum value. Hence for some position of *er* (for some particular coefficient of friction) the work spent in friction would be a maximum. What this value of the coefficient is it is impossible to say; but it seems to be less than that between clean india-rubber and iron, and it may be less than that between blackleaded india-rubber and iron. This was shown by the experiments on rolling-friction.

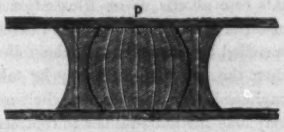
In considering these experiments, however, there is another thing to be taken into account besides the work spent in friction during compression, and that is the effect of friction during restitution; for the action of a roller as it passes over the india-rubber will be first to compress it and then to allow it to expand again in a corresponding manner.

The effect of Friction during Expansion.

If, after the rubber has been compressed as shown in figs. 4 and 5, the surfaces gradually separate again, the shape of the lines will again change. The lines from P up to *er* will assume the same forms which they had at corresponding periods of the

compression; but since that portion of the surface which lies beyond *er* has been extended by the compression, it will have to contract as the surfaces recede, and the friction of the surface will oppose such contraction. Hence the lines which during compression were curved outwards will gradually straighten and curve inwards, as shown in fig. 6. Those at the edges will take the form first, and then those nearer to *er*, until the expansion has become complete.

Fig. 6.



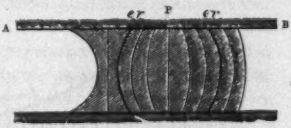
The extent to which friction will deform the india-rubber during this operation will obviously depend on the extent to which friction has allowed the surfaces to expand during compression. The smaller the friction the greater will be this expansion, and consequently the further they will have to contract, and the greater will be the pressure under which contraction must take place. It is obvious, therefore, that the work spent in friction during the recoil will increase up to a certain point as the coefficient of friction diminishes; and it would appear to be this increase which mainly balances the advantage which is gained during compression by reducing the coefficient.

It is evident that the action of friction to prevent contraction during restitution will tend to reduce not only the mean pressure but also the whole pressure, for exactly the same reason as by preventing expansion the friction increases these pressures during compression. Therefore, for every distance between the plates, after the curves become inclined inwards the pressure on the surface would be less than at the same distance with no friction, and in a still greater degree than during compression with friction. We can see at once, therefore, that of the work spent in compressing the material only a part would be returned during restitution. The difference is what is spent in overcoming the friction.

The Direction of the Friction.

In figures 5 and 6 the direction of slipping is opposite on opposite sides of P. If however, we conceive one half of the bar, that towards A, to have been compressed and to be expanding again, while the other half, that towards B, is being compressed and the distance between the plates which hold both parts to be the same, we may imagine the plate A B to have been first inclined towards A and then towards B so as to raise the end A. Then the lines would assume the form shown in fig. 7.

Fig. 7.



In this case we see that the slipping takes place in the same direction on both sides of P, so that the top plate A B would slip backwards in direction A over the india-rubber, while, on the other hand, the india-rubber would slip forwards in the direction D over the lower plate.

The turning of the plate A B, which has been supposed to be going on in figure 7, represents very closely the action of a roller in compressing the material beneath it; and this case affords us an illustration of the way in which the lateral extension of the material under the roller, or of the roller itself, will by causing slipping alter the distance travelled by the roller. If the roller be hard and the surface on which it rolls soft, then the top plate A B may be taken to represent the roller, and, as has just been explained, this slips back; whereas if the roller be soft and the surface hard, then we may take the india-rubber to represent the roller, and this slips forward.

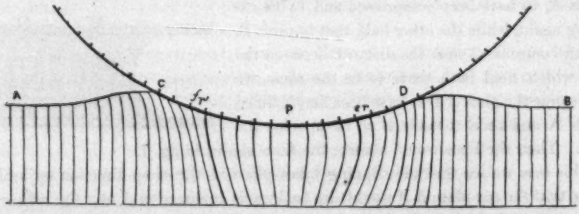
A Continuous Surface.

It is clear that in the case of the bar shown in fig. 7 the slipping will diminish as the coefficient of friction increases. There is, however, an important difference between this case and that of a roller in which it is not the entire breadth of a bar that is compressed, but a portion of a continuous surface; for whatever lateral extension there may be immediately under the roller must be compensated by a lateral compression immediately in front and behind it. The greater the lateral extension under the roller the greater will be the lateral compression; and since the action of the roller is continually to change the one for the other, the one effect will to a certain extent counteract the other; so that in this case we need not expect to find the diminution attended with a corresponding increase in the ostensible slipping. This will be rendered clearer by examining these circumstances as they affect rolling.

The Deformation caused by a Roller.

Fig. 8 may be taken to represent a section of an iron cylinder on an india-rubber plane. The lines on the plane are supposed to represent lines initially vertical and at equal distances apart. The motion of the roller is towards B. P is the point of greatest compression directly below the centre of the roller; er and fr limit the surfaces over which there is no slipping; D is the point at which contact commences, and C that at which it ceases.

Fig. 8.



The portions of the india-rubber immediately without C and D are laterally compressed;

this, as has already been pointed out, is to make room for the lateral extension under the roller from C to D. From D towards B, therefore, and from C towards A the parallel lines are somewhat distorted, and at something less than their natural distance apart. From D to er vertical compression and lateral expansion is going on, and the lines are convex outwards. From er to P there is no slipping and the lines straighten. From P to fr, which is greater than the corresponding distance from P to er, there is no slipping, and at fr the lines are convex outwards. From fr to C vertical expansion and lateral contraction take place, so that the lines are all concave outwards. The lateral expansion from D to er and the lateral contraction from fr to C can only take place by the slipping of the india-rubber over the iron. Its extent is shown by the distance between the corresponding lines on the india-rubber and those on the iron, which latter have been set out equal to the distance between the lines on the rubber where greatest, namely from er to fr.

The Actual and Apparent Slipping.

Since there is no slipping at P, it is clear that the roller will roll through less than its geometrical distance, inasmuch as the geometrical distance between the lines on the plane at P is greater than their natural distance. Therefore the ostensible slipping will be equal to the difference between the intervals marked on the roller, and the initial distance between those on the rubber. The actual slipping, however, is equal to the difference between the intervals on the roller and the intervals on the rubber at D or C, which latter are less than the natural distance; therefore the actual slipping is greater than the ostensible in proportion to the compression at C and D; and since this is increased by diminishing the coefficient of friction, such a diminution will affect the actual slipping in a greater degree than it affects the ostensible. This is in accordance with what has already been stated.

India-rubber Roller.

If the distance between the lines at P were exactly equal to the natural distance, then the roller would roll through its geometrical distance whatever might be the actual slipping. This is very nearly what actually takes place when an india-rubber roller rolls on an iron plane.

In the case of an india-rubber roller on an india-rubber surface the lateral compression in the surface of the roller at D is greater than that in the plane, and the expansion at P is not so large, and hence there is slipping, and the roller will not accomplish its geometrical distance.

In this explanation I have referred to india-rubber because it is much more easy to conceive the effects on it than on a hard substance like iron, the expansion and contraction of which is quite inappreciable to our senses; the reasoning, however, applies equally well to all elastic substances, and is quite independent of their hardness or softness. That friction is sufficient to prevent the expansion of iron at a surface against which it

is squeezed out is amply proved by the fact that when a block of iron, hot or cold, is squeezed on an anvil the iron bulges out in the middle, as shown in fig. 4.

Experimental Verification of the Figures.

The figures which illustrate the foregoing remarks are not altogether ideal, for they have been verified to a certain extent by experiments on india-rubber; for instance, by drawing vertical lines on the edge of a plate of india-rubber, and then observing these lines as the roller passed along as near as possible to this edge; also by observing lines drawn in the same way on the edge of an india-rubber roller. The effect of friction to prevent expansion, shown in figures 4 and 5, was verified by marking the surface of the india-rubber under the plate A B with parallel lines in chalk, which left a mark on the iron and showed how far there had been slipping. The figures are nevertheless intended rather to illustrate the nature of the slipping and various effects than their extent, which latter must be judged of by the experimental results which I now proceed to describe.

The Experiments.

My first object in making these experiments was to ascertain if, and how, oiling the surfaces in contact affected the resistance to rolling.

The apparatus employed consisted of a wooden slab or table-top supported on three set-screws for legs, so that it could be tipped in any required direction. On this table rested one of WHITWORTH'S surface-plates. On the surface-plate was placed a surveyor's level, which read divisions to the thousandth of a foot on a staff erected at 50-feet distance; also a bell-glass covered another part of the surface-plate in the manner of the receiver of an air-pump, which could be filled with oil from an aperture in the top. This glass served either to protect the roller from dust or surround it with oil, and thus prevent any surface-tension the oil might exert affecting the results.

The roller was of cast iron, 6 inches in diameter and 2 inches thick, and weighed about 14 lbs. It was not cylindrical, for the edge was somewhat rounded. Originally the roller was turned up so that the edge was curved to a radius of 1 foot; but subsequent grinding somewhat modified this shape.

In the first instance the roller was turned up and polished in the ordinary manner; but some preliminary experiments showed that the surface thus formed was far from perfect, as indeed was apparent when it was examined with a magnifying-glass. The roller was therefore again turned and ground very carefully with Turkey-stone for several days, until the surface appeared through the glass to be as perfect as the iron would allow; there were still some small pits, but these appeared to be in the iron itself.

The roller when thus finished was rolled on various surfaces. First of all it was tried on the cast-iron surface-plate already mentioned; but this surface, which had been formed by scraping, was altogether too rough. Thus when the roller was placed on the plate it immediately rolled into a hollow. Surfaces were then formed by grinding

two plates together with powdered Turkey-stone. In this way the plates were made so true that the roller would remain in any position, and would roll either way with an inclination of 1 in 5000, or about 1 foot in a mile. It appeared impossible, however, to produce surfaces altogether free from inequalities, which may be seen from the results of the experiments.

The effect of Oiling the Surface.

In the first experiments the surface on which the roller was to roll was brought into a level position, so that the roller when placed on it remained at rest. A line of sights, consisting of a mark on the glass and a pin-hole in a plate fixed at some distance, was then brought to bear on a mark on the top of the roller, so that the least motion could be detected, and the position of the roller could be recovered after it had been allowed to roll in one direction. The level was then adjusted to read zero on the staff, and the table tipped until the roller rolled off in one direction. The reading of the level was then noted, and the same operation repeated in the opposite direction, the roller having in the mean time been brought back into its former position. Sundry observations were then taken with different points of the plane and roller in contact. After a considerable number of observations had thus been taken oil was poured into the glass until the roller was covered, and then the observations were repeated. Table I. shows a series of

TABLE I.—Cast-iron Roller on Plate-glass. (The distance of the Staff from the Object-glass of the Level = 50 feet. The Divisions on the Scale = $\frac{1}{100}$ foot.)

	Clean.			Oiled.		
	Readings.		Difference.	Readings.		Difference.
	To.	From.		To.	From.	
Starts from rest.	−5·0	1·2	6·2	−5·0	3·2	8·2
	−2·3	3·5	5·8	−3·3	2·5	5·8
	−2·6	2·0	4·6	−4·0	2·0	6·0
	−4·5	1·4	5·9	−4·1	1·0	5·1
	−4·7	2·0	6·7	−1·8	4·0	5·8
	−2·8	3·5	6·3	−3·0	2·0	5·0
	−3·2	4·5	7·7	−5·8	0·5	6·3
	−4·0	3·4	7·4	−5·2	0·3	5·5
	Mean.....		6·3	Mean.....		5·9
Rolls back when set in motion.	−2·6	−0·7	1·9	−3·0	−0·4	2·6
	−3·5	−1·5	2·0	−1·8	+1·0	2·8
	−3·5	−2·0	1·5	−2·5	0·0	2·5
	−4·2	−2·2	2·0	−2·5	+0·2	2·7
	−1·5	+0·6	2·1	−3·9	−1·0	2·9
	−2·5	−0·5	2·0	−3·0	−0·8	2·2
	−1·9	0·0	1·9	−4·4	−2·0	2·4
	−0·7	+1·5	2·1	−1·0	+1·5	2·5
	Mean.....		1·9	Mean.....		2·6

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such observations for a surface of plate-glass both with and without oil. In these particular experiments, however, the surface was simply oiled, it having been found by experience that the effect was the same as when the glass was filled with oil. It will be seen that in these experiments the advantage is slightly in favour of the oiled glass.

The results contained in the second part of this Table were obtained by starting the roller in one direction against the inclination of the plane with just sufficient velocity to carry it up to a certain point, the inclination of the plane being adjusted until it would roll back. In this way the advantage is against the oil. This, however, I think is due to the surface-tension or fluid-friction arising from the motion of the roller.

There is a very marked difference between these inclinations and those required to start the roller from rest, a difference which appears to exist with all the materials tried, and which I think is only in part explained by the roughness of the surface.

In these experiments with a surface of glass the friction was so small that the inequalities of the surface rendered the results very irregular and uncertain. To obviate this a surface of box-wood cut across the grain was next tried. This, being softer, allowed the roller to indent it more than the glass and gave rise to greater friction, and hence the inequalities in the surface are less apparent in the results, which are shown in Table II. These observations were made in the same way as those with the glass, except that *blacklead* was substituted for oil. The effect of the blacklead seems to

TABLE II.—Cast-iron Roller on Box-wood.

	Clean.			Blackleaded.		
	Readings.		Difference.	Readings.		Difference.
	To.	From.		To.	From.	
Starts from rest.	− 3·0	+ 5·0	8·0	−4·8	+ 6·0	10·8
	− 3·0	+ 8·0	11·0	−3·2	+ 7·8	11·0
	− 4·0	+ 5·8	9·8	−7·6	+ 2·4	10·0
	− 4·0	+ 6·0	10·0	−0·5	+ 8·0	8·5
	−10·0	0·0	10·0	+0·8	+10·0	9·2
	+ 3·4	+12·8	9·4	+1·0	+ 8·9	7·9
	− 4·0	+ 7·0	11·0	−9·0	− 1·2	7·8
	− 3·2	+ 8·0	11·2	−9·8	− 1·0	8·8
	Mean		10·05	Mean.....		9·25
Rolls back when set in motion.	+7·0	+12·2	5·2	−1·0	+1·0	3·5
	−5·0	+ 0·4	5·4	−1·2	+1·2	4·0
	−2·0	+ 4·2	6·2	0·0	+2·0	2·0
	−2·1	+ 3·8	5·9	+2·0	+5·0	3·0
	+3·2	+ 9·0	5·8	+1·2	+4·0	2·8
	+1·3	+ 7·0	5·7	+3·0	+6·2	3·2
	−2·0	+ 4·0	6·0	−6·4	−3·0	3·6
	−2·6	+ 2·9	5·5	−7·6	−3·0	4·6
	Mean.....		5·71	Mean.....		3·34

have been slightly to diminish friction, not only when starting from rest, but when rolling back, which confirms me in the opinion that the contrary result with oil was due to its obstructive action.

India-rubber was then tried. A plate of this substance three eighths of an inch thick was glued to a piece of wood to prevent it working forward. The results are shown in Table III. The friction was very much greater than in the previous experiments, and the advantage lies with the clean surface.

TABLE III.—Cast-iron Roller on India-rubber.

	Clean.			Blackleaded.		
	Readings.		Difference.	Readings.		Difference.
	To.	From.		To.	From.	
Starts from rest.	−22·0	+14·0	36	−24	+18	42
	−28·0	+15	43	−19	+15	34
	−12·0	+18	30	−18	+19	37
	−19·0	+15	34	−23	+17	40
	−16·0	+16	32	−22	+17	39
	−18·0	+15	33	−23	+14	37
	−25·0	+12	37	−25	+17	42
	−23·0	+15	38	−24	+15	39
	Mean.....		35·3	Mean		38·75
Rolls back when set in motion.	−2	+28	30	0	+26	26
	−5	+26	31	− 2	+22	24
	−6	+27	33	− 1	+25	26
	−4	+28	32	− 2	+22	24
	−3	+30	33	−10	+22	32
	−4	+30	34	−14	+19	33
	−6	+24	30	− 6	+24	30
	−7	+25	32	− 6	+23	29
	Mean.....		31·8	Mean		28

These results leave no doubt that rolling-friction does not depend greatly on the coefficient of sliding-friction between the roller and the surface. They are, however, completely in accordance with the explanation previously given of the manner in which sliding-friction acts to prevent the deformation of the surfaces at the point of contact.

The Tendency to Oscillate.

Another circumstance which was observed while making these experiments also offers strong evidence of this deformation, namely the tendency which the roller has to oscillate. This was always exhibited whenever the roller was slightly disturbed from rest on the level plane, and it was certainly not due to the fact of its having settled into a hollow; for when on india-rubber it would make several considerable oscillations in *whatever*

position it was placed. By blackleading the surface this tendency was considerably reduced, although not altogether destroyed. These oscillations could not have been caused by the mere resistance which the one surface offered to the sliding of the other over it, unless also this resistance threw the surfaces into constraint from which they are constantly endeavouring to free themselves.

The effect of the Softness of the Materials.

Having found that oil did not reduce the resistance, the experiments were continued with a view to ascertain how far the softness of the material had any thing to do with it. As materials of several degrees of softness had already been tried, the only question was to settle how far the difference in the results observed was due to their softness and how far it might be due to some other difference in their nature. To show this cast iron and brass were tried, which are of much the same hardness as glass, and yet of an altogether different nature in other respects, the surface of the glass being highly polished, while that of the metal was dull as it had been left by the grinding. The results of these experiments are contained in Tables IV. and V.

TABLE IV.—Cast-iron Roller on Brass.

	Clean.			Oiled.		
	Readings.		Difference.	Readings.		Difference.
	To.	From.		To.	From.	
Starts from rest.	−13·2	−5·5	7·7	−2·0	+3·8	5·8
	− 5·5	+2·0	7·5	−4·5	+1·2	5·7
	− 3·2	+5·0	8·2	−2·8	+3·8	6·6
	− 3·5	+4·5	8·0	−2·9	+5·2	8·1
	− 3·5	+3·8	7·3	−1·7	+5·8	7·5
	− 7·0	+1·5	8·5	−5·0	+1·0	6·0
	− 5·0	+2·2	7·2	−3·0	+3·5	6·5
	− 4·6	+3·0	7·6	−3·0	+2·9	5·9
	Mean		7·75	Mean.....		6·5
Rolls back when set in motion.	−2·4	−0·8	1·6	−1·5	+1·0	2·5
	−2·4	−0·4	2·0	0·0	+1·8	1·8
	−1·8	+0·7	2·5	−1·2	+1·6	2·8
	−2·0	−0·4	1·6	−2·0	+0·6	2·6
	−2·8	−1·0	1·8	−2·3	+0·5	2·8
	−2·5	+0·2	2·7	−2·0	+1·0	3·0
	−0·2	+2·0	2·2	−1·2	+1·5	2·7
	−2·2	0·0	2·2	−0·9	+1·6	2·5
	Mean		2·07	Mean		2·58

The means of the results for all the materials are contained in Table VI. Comparing these we see at once the effect of softness: the cast iron, brass, and glass are very nearly the same, and the slight difference is not greater than may be accounted for by a slight

TABLE V.—Cast-iron Roller on Cast Iron.

	Clean.			Oiled.		
	Readings.		Difference.	Readings.		Difference.
	To.	From.		To.	From.	
Starts from rest.	−6·5	+0·3	6·8	−1·3	+4·0	5·3
	−2·8	+2·4	5·2	−2·8	+2·5	5·3
	−2·6	+3·5	6·1	−3·5	+2·5	6·0
	−2·5	+2·3	4·8	−2·5	+3·8	6·3
	−0·6	+4·5	5·1	−2·2	+3·2	5·4
	−0·9	+3·9	4·8	−2·3	+3·0	5·3
	−3·0	+2·5	5·5	−5·0	+0·8	5·8
	−2·8	+4·2	7·0	+1·0	+6·5	5·5
	Mean		5·66	Mean		5·61
Rolls back when set in motion.	+4·0	+6·5	2·5	0·0	+2·3	2·3
	−0·7	+1·6	2·3	−1·8	+0·8	2·6
	−3·5	−0·8	2·7	−1·0	+1·3	2·3
	−3·8	−1·0	2·8	+0·2	+2·3	2·1
	−0·5	+1·8	2·3	0·0	+2·2	2·2
	−2·0	+0·1	2·1	−0·6	+2·0	2·6
	−0·8	+2·2	3·0	−0·6	+1·8	2·4
	−1·3	+1·6	2·9	+0·5	+2·9	2·4
	Mean		2·57	Mean		2·36

difference in the smoothness of the surfaces. Of the three, according to hardness cast iron should have given the least results; and so it does, as far as starting from rest is concerned, although when rolling back the result is the other way. Box-wood appears to offer about double the resistance of cast iron; and india-rubber about ten times as much in the case of rolling back, and six times as much in starting from rest.

TABLE VI.—Showing the Mean of the Results for the various conditions of the Surface and manner of Starting.

The nature of the Surface.	Starts from rest.		Started in the opposite direction.		Mean.
	Clean.	Oiled or blackleaded.	Clean.	Oiled or blackleaded.	
Cast iron	5·66	5·61	2·57	2·36	4·05
Glass	6·32	5·96	1·93	2·56	4·19
Brass	7·75	6·53	2·07	2·587	4·73
Box-wood	10·05	9·25	5·71	2·34	7·09
India-rubber	35·37	38·75	31·87	28·00	33·24

Experiments on Actual Slipping.

My object in the second series of experiments was to find by actual measurement how far the roller rolled short of its geometrical distance. Since the exceedingly small slipping on a hard surface precluded all chance of measuring it, these experiments were made on strips of india-rubber glued to wood: these were in general long enough to allow of two complete revolutions of the roller. The strips were of different thicknesses. This difference of thickness has an effect to vary the degree of indentation and the intensity of the pressure, as well as the lateral extension. On the thick india-rubber the indentation was considerable; and, owing to the large bearing-surface thus obtained, the intensity of the pressure beneath the roller must have been comparatively small, as must also the lateral extension; whereas with the thin strips the indentation was small, but the pressure and consequent lateral extension must have been correspondingly great. These considerations serve to explain the differences in the results of the experiments, which are given in Tables VII. and VIII.

TABLE VII.—Showing the Actual Slipping of a Cast-iron Roller.

The nature of the Surface.	The distance travelled.		The amount of the slipping.
	In one revolution.	In two revolutions.	
A steel bar (polished)	17·82	35·64	·00
India-rubber, 0·015 inch thick, glued to wood	....	35·2	·44
Ditto, 0·08 inch thick	....	34·8	·84
Ditto, 0·36 inch thick	....	35·15	·49

TABLE VIII.—Showing the Actual Slipping with an India-rubber Tire 0·75 inch thick glued on to the Roller.

The nature of the Surface.	Distance travelled in one revolution.	Circumference of the ring.	The amount of the slipping.
A steel bar	22·55	22·5	−0·05
India-rubber 0·156 inch thick (clean)	22·55	,,	−0·05
,, ,, (blackleaded)	22·55	,,	−0·05
,, 0·08 inch thick (clean)	22·5	,,	0·0
,, ,, (blackleaded)	22·52	,,	−0·02
,, 0·36 inch thick (clean)	22·39	,,	+0·11
,, ,, (blackleaded)	22·42	,,	+0·08
,, 0·75 inch thick (clean)	22·4	,,	+0·1
,, ,, (blackleaded)	22·4	,,	+0·1

These experiments show that a hard roller on a soft surface rolls short of its geometrical distance, whereas a soft roller on a hard plane rolls more than its geometrical distance, but to a smaller degree, and that when the roller and the plane are of equal hardness the roller rolls through less than its geometrical distance, which results are in exact accordance with what has previously been explained.

The effect of Heat and Viscosity to cause Friction.

While making the experiments which have been described, two other causes of resistance to rolling besides friction suggested themselves to me, and were to a certain extent verified. The first of these is the transference of heat which takes place within both the plate and the roller in the neighbourhood of the point of contact. As the roller moves forward it is continually compressing the material in front of the point of greatest pressure, and this material expands again so soon as the roller is past. During compression there will be a change in the temperature of the material compressed, which change will be readjusted again as the material expands, supposing that in the interval between compression and expansion there has been no heat communicated to or taken from the portion of material affected. But since the change of temperature caused by compression will place the part compressed out of accord with that immediately surrounding it, a transference of heat will necessarily take place. The quantity of heat thus transferred will depend on the length of the interval, *i. e.* the speed of the roller, and on the conducting-power of the material.

This transference will cause resistance to the roller, for the material will not expand to the same temperature, and hence to the same volume, as that from which it was compressed, and hence it will take more work to compress it than it will give out in expanding.

It does not, however, follow that the greater the transference of heat the greater the resistance; for if a sufficient time be allowed the transference of heat will readjust the temperature as fast as expansion takes place. There is some speed, therefore, for which the resistance arising from this cause will be a maximum. If, therefore, the material be a good conductor and the motion slow, the transference of heat will prevent any variation of temperature during either compression or expansion. When such was the case the resistance would increase with the speed, a fact which was very evident when the rolling took place on india-rubber; for it was possible to give the plane such an inclination that the motion of the roller was scarcely perceptible, and any increase in the inclination was followed by a corresponding increase in the speed of the roller.

As already stated, there is another cause of resistance; and this may partly explain the result: this is viscosity.

If we stretch a piece of india-rubber, or any material, when released it does not *immediately* come back to its original length, but at once comes back a certain distance and then recovers the rest more or less slowly. Hence as the roller moves forward the compressed material will require time for its complete expansion, and hence will offer less resistance to the roller when the motion is slow than when it is rapid.

Conclusion.

The foregoing remarks must be regarded as relating only to the *nature* of rolling-friction. I have not attempted to ascertain the laws which connect its magnitude with the various circumstances which affect it. As far as they go I can see no reason to doubt

the two laws propounded by COULOMB, viz. that for the same material the resistance to rolling is proportional to the weight of the roller, and inversely proportional to its diameter. In addition to these laws, however, it appears clear to me that there must be another law connecting rolling-friction in some way with the softness of the tires of the wheels and the road. In addition to the instance of india-rubber tires already mentioned, there are several other phenomena connected with wheels which point to such a law, and can be explained by the recognition of the slipping under the roller.

Steel and Iron Rails.

The very great advantage in point of durability of steel rails over iron has been a matter of much surprise, it not being sufficiently accounted for by the greater hardness of the steel, supposing it to be subjected to the same wearing action as the iron. This is at once explained, however, by the recognition of the fact that hardness tends to reduce the slipping and hence the wearing action, as well as to enable the rail the better to withstand the wear to which it is subjected.

That rails should wear at all in places where they are straight and where brakes are not applied is a matter which calls for an explanation, and this, so far as I am aware, has not hitherto been given; mere crushing, however much it might deform the rail, would not cause such a reduction of weight as actually takes place. The explanation of this phenomenon also at once follows the recognition of the slipping which attends rolling.

A little consideration also serves to show that the scaling of wrought-iron rails is the result of the repeated lateral extension of the surface of the rail under the action of the wheel. The systematic way in which this takes place shows that it is due to something more than the mere imperfection in the iron. There is no doubt that the grain of the iron has a great deal to do with it; but considering the multitudinous ways in which iron is used and that this is the only one in which scaling takes place, it is clear that it must be due to some cause directly connected with the action to which the rail is subjected. Now every time a wheel passes over a point in a rail it tends to slide the upper strata of the rail over those beneath them, and thus causes tangential stress. If the rail were homogeneous this would hardly cause it to scale; but owing to the grain in the iron some strata are stronger than others, and the weaker strata are called upon to do more than their share of the yielding, and so become still weaker and eventually give way.

There are other phenomena which, having been hitherto unnoticed or unexplained, might be shown to arise from the slipping which takes place during rolling; but perhaps those I have mentioned are sufficient to show that the effects of the action are not altogether without practical importance.

II. *On the Development of the Spinal Nerves in Elasmobranch Fishes.* By F. M. Balfour, *B.A., Fellow of Trinity College, Cambridge.* *Communicated by Dr.* Michael Foster, *F.R.S., Prælector in Physiology and Fellow of Trinity College, Cambridge.*

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In the course of an inquiry into the development of Elasmobranch Fishes, my attention has recently been specially directed to the first appearance and early stages of the spinal nerves, and I have been led to results which differ so materially from those of former investigators that I venture at once to lay them before the Society. I have employed in my investigations embryos of *Scyllium canicula*, *Scyllium stellare*, *Pristiurus*, and *Torpedo*. The embryos of the latter animal, especially those hardened in osmic acid, have proved by far the most favourable for my purpose, though, as will be seen from the sequel, I have been able to confirm the majority of my conclusions on embryos of all the above-mentioned genera.

A great part of my work was done at the Zoological Station founded by Dr. Dohrn at Naples; and I have to thank both Dr. Dohrn and Dr. Eisig for the uniformly obliging manner in which they have met my requirements for investigation. I have more recently been able to fill up a number of lacunæ in my observations by the study of embryos bred in the Brighton Aquarium; for these I am indebted to the liberality of Mr. Lee and the Directors of that institution.

The first appearance of the Spinal Nerves in Pristiurus.

In a *Pristiurus*-embryo, at the time when two visceral clefts become visible from the exterior (though there are as yet no openings from without into the throat), a transverse section through the dorsal region exhibits the following features (Plate 16. fig. A):—

The external epiblast is formed of a single row of flattened elongated cells. Vertically above the neural canal the cells of this layer are more columnar and form the rudiment of the primitively continuous dorsal fin.

The neural canal (*nc*) is elliptical in section, and its walls are composed of oval cells two or three deep. The wall at the two sides is slightly thicker than at the ventral and dorsal ends, and the cells at the two ends are also smaller than elsewhere. A typical cell from the side walls of the canal is about $\frac{1}{1000}$ inch in its longest diameter. The outlines of the cells are for the most part distinctly marked in the specimens hardened in either chromic or picric acid, but more difficult to see in those prepared with osmic acid; their protoplasm is clear, and in the interior of each is an oval nucleus very large in proportion to the size of its cell. The long diameter of a typical nucleus is about $\frac{1}{3000}$ inch, or about two thirds of that of the cell.

The nuclei are granular, and very often contain several especially large and deeply stained granules; in other cases only one such is present, which may then be called a nucleolus.

In sections there may be seen round the exterior of the neural tube a distinct hyaline membrane: this becomes stained of a brown colour with osmic acid, and purple or red with hæmatoxylin or carmine respectively. Whether it is to be looked upon as a distinct membrane differentiated from the outermost portion of the protoplasm of the cells, or as a layer of albumen coagulated by the reagents applied, I am unable to decide for certain. It makes its appearance at a very early period, long before that now being considered; and similar membranes are present around other organs as well as the neural tube. The membrane is at this stage perfectly continuous round the whole exterior of the neural tube *as well on the dorsal surface as on the ventral.*

The section figured, whose features I am describing, belongs to the middle of the dorsal region. Anteriorly to this point the spinal cord becomes more elliptical in section, and the spinal canal more lanceolate; posteriorly, on the other hand, the spinal canal and tube become more nearly circular in section. Immediately beneath the neural tube is situated the notochord (*ch*). It exhibits at this stage a central area rich in protoplasm, and a peripheral layer very poor in protoplasm; externally it is invested by a distinct cuticular membrane.

Beneath the notochord is a peculiar rod of cells, constricted from the top of the alimentary canal*. On each side and below this are the two aortæ, just commencing to be formed, and ventral to these is the alimentary canal.

On each side of the body two muscle-plates are situated; their upper ends reach about one third of the way up the sides of the neural tube. The two layers which together constitute the muscle-plates are at this stage perfectly continuous with the somatic and splanchnic layers of the mesoblast, and the space between the two layers is continuous with the body-cavity. In addition to the muscle-plates and their ventral continuations, there are no other mesoblast-cells to be seen. The absence of all mesoblastic cells dorsal to the superior extremities of the muscles is deserving of special notice.

Very shortly after this period and, as a rule, before a third visceral cleft has become visible, the first traces of the spinal nerves make their appearance.

First Stage.—The spinal nerves do not appear at the same time along the whole length of the spinal canal, but are formed first of all in the neck and subsequently at successive points posterior to this.

Their mode of formation will be most easily understood by referring to Plate 16. figs. B I, B II, B III, which are representations of three sections taken from the same embryo. B I is from the region of the heart; B II belongs to a part of the body posterior to this, and B III to a still posterior region.

* *Vide* Balfour, "Preliminary account of the Development of Elasmobranch Fishes," Quart. Journ. of Microsc. Science, Oct. 1874, p. 33.

In most points the sections scarcely differ from Plate 16. fig. A, which, indeed, might very well be a posterior section of the embryo to which these three sections belong.

The chief point, in addition to the formation of the spinal nerves, which shows the greater age of the embryo from which the sections were taken is the complete formation of the aortæ.

The upper ends of the muscle-plates have grown no further round the neural canal than in fig. A, and no scattered mesoblastic connective-tissue cells are visible.

In fig. A the dorsal surface of the neural canal was as completely rounded off as the ventral surface; but in fig. B III this has ceased to be the case. The cells at the dorsal surface of the neural canal have become rounder and smaller and begun to proliferate, and the uniform outline of the neural canal has here become broken (fig. B III, *pr*). The peculiar membrane completely surrounding the canal in fig. A now terminates just below the point where the proliferation of cells is taking place.

The prominence of cells which springs in this way from the top of the neural canal is the commencing rudiment of a pair of spinal nerves. In fig. B II, a section anterior to fig. B III, this formation has advanced much further (fig. B II, *pr*). From the extreme top of the neural canal there have now grown out two club-shaped masses of cells one on each side; they are perfectly continuous with the cells which form the extreme top of the neural canal, and necessarily also are in contact with each other dorsally. Each grows outwards in contact with the walls of the neural canal; but, except at the point where they take their origin, they are not continuous with its walls, and are perfectly well separated by a sharp line from them.

In fig. B I, though the club-shaped processes still retain their attachment to the summit of the neural canal, they have become much longer and more conspicuous.

Specimens hardened in both chromic acid (Plate 16. fig. C) and picric acid give similar appearances as to the formation of these bodies.

In those hardened in osmic acid, though the mutual relations of the masses of cells are very clear, yet it is difficult to distinguish the outlines of the individual cells.

In the chromic-acid specimens (fig. C) the cells of these rudiments appear rounded, and each of them contains a large nucleus.

I have been unable to prepare longitudinal sections of this stage, either horizontal or vertical, to show satisfactorily the extreme summit of the spinal cord; but I would call attention to the fact that the cells forming the proximal portion of the outgrowth are seen in every transverse section at this stage, and therefore exist the whole way along, whereas the *distal* portion is seen only in every third or fourth section, according to the thickness of the sections. It may be concluded from this that there appears a continuous outgrowth from the spinal canal, from which discontinuous processes grow out.

In specimens of a very much later period (Plate 18. fig. L) the proximal portions of the outgrowth are unquestionably continuous with each other, though their actual junctions with the spinal cord are very limited in extent. The fact of this continuity at a later period is strongly in favour of the view that the posterior branches of the spinal nerves

arise from the first as a continuous outgrowth of the spinal cord, from which a series of distal processes take their origin. I have, however, failed to demonstrate this point absolutely. The processes, which we may call the nerve-rudiments, are, as appears from the later stages, equal in number to the muscle-plates.

It may be pointed out, as must have been gathered from the description above, that the nerve-rudiments have at this stage but one point of attachment to the spinal cord, and that this one corresponds with the dorsal or posterior root of the adult nerve.

The rudiments are, in fact, those of the posterior root only.

The next or second stage in the formation of these structures to which I would call attention occurs at about the time when three to five visceral clefts are present. The disappearance from the notochord in the anterior extremity of the body of a special central area rich in protoplasm serves as an excellent guide to the commencement of this epoch.

Its investigation is beset with far greater difficulties than the previous one. This is owing partly to the fact that a number of connective-tissue cells, which are only with great difficulty to be distinguished from the cells which compose the spinal nerves, make their appearance around the latter, and partly to the fact that the attachment of the spinal nerves to the neural canal becomes much smaller, and therefore more difficult to study.

Fortunately, however, in *Torpedo* these peculiar features are not present to nearly the same extent as in *Pristiurus* and *Scyllium*.

The connective-tissue cells, though they appear earlier in *Torpedo* than in the two other genera, are much less densely packed, and the large attachment of the nerves to the neural canal is retained for a longer period.

Under these circumstances I consider it better, before proceeding with this stage, to give a description of the occurrences in *Torpedo*, and after that to return to the history of the nerves in the genera *Pristiurus* and *Scyllium*.

The development of the Spinal Nerves in Torpedo.

The youngest *Torpedo*-embryo in which I have found traces of the spinal nerves belongs to the earliest part of what I called the second stage.

The segmental duct* is just appearing, but the cells of the notochord have not become completely vacuolated. The rudiments of the spinal nerves extend half of the way towards the ventral side of the spinal cord; they grow out in a most distinct manner from the dorsal surface of the spinal cord (Plate 16. fig. D a, *pr*); but the nerve-rudiments of the two sides are no longer continuous with each other at the dorsal median line, as in the earlier *Pristiurus*-embryos. The cells forming the proximal portion of the rudiment have the same elongated form as the cells of the spinal cord, but the remaining cells are more circular.

* *Vide* Balfour, "Origin and History of Urino-genital Organs of Vertebrates," Journal of Anatomy and Physiology, Oct. 1875.

From the summit of the muscle-plates (*mp*) an outgrowth of connective-tissue has made its appearance (*c*), which eventually fills up the space between the dorsal surface of the cord and the external epiblast. There is not the slightest difficulty in distinguishing the connective-tissue cells from the nerve-rudiment. I believe that in this embryo the origin of the nerves from the neural canal was a continuous one, though naturally the peripheral ends of the nerve-rudiments were separate from each other.

The most interesting feature of the stage is the commencing formation of the anterior roots. Each of these arises (Plate 16. fig. D a, *ar*) as a small but distinct outgrowth from the epiblast of the spinal cord, near the ventral corner of which it appears as a conical projection. Even from the very first it has an indistinct form of termination and a fibrous appearance, while the protoplasm of which it is composed becomes very attenuated towards its termination.

The points of origin of the anterior roots from the spinal cords are separated from each other by considerable intervals. In this fact, and also in the nerves of the two sides never being united with each other in the ventral median line, the anterior roots exhibit a marked contrast to the posterior.

There exists, then, in *Torpedo*-embryos by the end of this stage distinct rudiments of both the anterior and posterior roots of the spinal nerves. These rudiments are at first quite independent of and disconnected with each other, and both take their rise as outgrowths of the epiblast of the neural canal.

The next *Torpedo*-embryo (Plate 16. fig. D b), though taken from the same female, is somewhat older than the one last described. The cells of the notochord are considerably vacuolated; but the segmental duct is still without a lumen. The posterior nerve-rudiments are elongated, pear-shaped bodies of considerable size, and, growing in a ventral direction, have reached a point nearly opposite the base of the neural canal. They still remain attached to the top of the neural canal, though the connexion has in each case become a pedicle so narrow that it can only be observed with great difficulty.

It is fairly certain that by this stage each posterior nerve-rudiment has its own separate and independent junction with the spinal cord; their dorsal extremities are nevertheless probably connected with each other by a continuous commissure.

The cells composing the rudiments are still round, and have, in fact, undergone no important modifications since the last stage.

The important feature of the section figured (fig. D b), and one which it shares with the other sections of the same embryo, is the appearance of connective-tissue cells around the nerve-rudiment. These cells arise from two sources; one of these is supplied by the vertebral rudiments, which at the end of the last stage (Plate 16. fig. C, *vr*) become split off from the inner layer of the muscle-plates. The vertebral rudiments have in fact commenced to grow up on each side of the neural canal, in order to form the mass of cells out of which the neural arches are subsequently developed.

The dorsal extremities of the muscle-plates form the second source of these connective-tissue cells. These latter cells lie dorsal and external to the nerve-rudiments.

The presence of this connective-tissue, in addition to the nerve-rudiments, removes the possibility of erroneous interpretations in the previous stages of the *Pristiurus*-embryo.

It might be urged that the two masses which I have called nerve-rudiments are nothing else than mesoblastic connective-tissue commencing to develop around the neural canal, and that the appearance of attachment to the neural canal which they present is due to bad preparation or imperfect observation. The sections of both this and the last *Torpedo*-embryo which I have been describing clearly prove that this is not the case. We have, in fact, in the same sections the developing connective-tissue as well as the nerve-rudiments, and at a time when the latter still retains its primitive attachment to the neural canal. The anterior root (fig. D b, *ar*) is still a distinct conical prominence, but somewhat larger than in the previously described embryo; it is composed of several cells, and the cells of the spinal cord in its neighbourhood converge towards its point of origin.

In a *Torpedo*-embryo (Plate 16. fig. D c) somewhat older than the one last described, though again derived from the oviduct of the same female, both the anterior and the posterior rudiments have made considerable steps in development.

In sections taken from the hinder part of the body I found that the posterior rudiments nearly agreed in size with those in fig. D b.

It is, however, still less easy than there to trace the junction of the posterior rudiments with the spinal cord, and the upper ends of the rudiments of the two sides do not nearly meet.

In a considerable series of sections I failed to find any case in which I could be absolutely certain that a junction between the nerve and the spinal cord was effected; and it is possible that in course of the change of position which this junction undergoes there may be for a short period a break of continuity between the nerve and the cord. This, however, I do not think probable. But if it takes place at all, it takes place before the nerve becomes functionally active, and so cannot be looked upon as possessing any physiological significance.

The rudiment of the posterior nerve in the hinder portion of the body is still approximately homogeneous, and no distinction of parts can be found in it.

In the same region of the body the anterior rudiment retains nearly the same condition as in the previous stage, though it has somewhat increased in size.

In the sections taken from the anterior part of the same embryo the posterior rudiment has both grown in size and also commenced to undergo histological changes by which it has become divided into a root, a ganglion, and a nerve.

The root (fig. D c, *pr*) consists of small round cells which lie close to the spinal cord, and ends dorsally in a rounded extremity.

The ganglion (*g*) consists of larger and more elongated cells, and forms an oval mass enclosed on the outside by the downward continuation of the root, having its inner side nearly in contact with the spinal cord.

From its ventral end is continued the nerve, which is of considerable length, and has a course approximately parallel to that of the muscle-plate. It forms a continuation of the root rather than of the ganglion.

Further details in reference to the histology of the nerve-rudiment at this stage are given later in this paper, in the description of *Pristiurus*-embryos, of which I have a more complete series of sections than of the *Torpedo*-embryos.

When compared with the nerve-rudiment in the posterior part of the same embryo, the nerve-rudiment last described is, in the first place, considerably larger, and has secondly undergone changes, so that it is possible to recognize in it parts which can be histologically distinguished as nerve and ganglion.

The developmental changes which have taken place in the anterior root are not less important than those in the posterior. The anterior root now forms a very conspicuous cellular prominence growing out from the ventral corner of the spinal cord (fig. D c, *ar*). It has a straight course from the spinal cord to the muscle-plate, and there shows a tendency to turn downwards at an open angle: this, however, is not represented in the specimen figured. The cells of which it is composed each contain a large oval nucleus, and are not unlike the cells which form the posterior rudiment. The anterior and posterior nerves are still quite unconnected with each other; and in those sections in which the anterior root is present the posterior root of the same side is either completely absent or only a small part is to be seen. The cells of the spinal cord exhibit a slight tendency to converge towards the origin of the anterior nerve-root.

In the spinal cord itself the epithelium of the central canal is commencing to become distinguished from the grey matter, but no trace of the white matter is visible.

I have succeeded in making longitudinal vertical sections of this stage, which prove that the ends of the posterior roots adjoining the junction with the cord are all connected with each other (Plate 16. fig. D d).

If the figure representing a transverse section of the embryo (fig. D c) be examined, or better still the figure of a section of the slightly older *Scyllium*-embryo (Plate 17. fig. H 1 or I 1), the posterior root will be seen to end dorsally in a rounded extremity, and the junction with the spinal cord to be effected, not by the extremity of the nerve, but by a part of it at some little distance from this.

It is from these upper ends of the rudiments beyond the junction with the spinal cord that I believe the commissures to spring which connect together the posterior roots.

My sections showing this for the stage under consideration are not quite as satisfactory as is desirable; nevertheless they are sufficiently good to remove all doubt as to the presence of these commissures.

A figure of one of these sections is represented (Plate 16. fig. D d). In this figure *pr* points to the posterior roots and *x* to the commissures uniting them.

In a stage somewhat subsequent to this I have succeeded in making longitudinal sections, which exhibit these junctions with a clearness which leaves nothing to be desired.

It is there effected (Plate 18. fig. L) in each case by a protoplasmic commissure with imbedded nuclei*. Near its dorsal extremity each posterior root dilates, and from the dilated portion is given off on each side the commissure uniting it with the adjoining roots.

Considering the clearness of this formation in this embryo, as well as in the embryo belonging to the stage under description, there cannot be much doubt that at the first formation of the posterior rudiments a continuous outgrowth arises from the spinal cord, and that only at a later period do the junctions of the roots with the cord become separated and distinct for each nerve.

I now return to the more complete series of *Pristiurus*-embryos, the development of whose spinal nerves I have been able to observe.

Second Stage of the Spinal Nerves in Pristiurus.

In the youngest of these (Plate 17. fig. E) the notochord has undergone but very slight changes, but the segmental duct has made its appearance, and is as much developed as in the *Torpedo*-embryo from which fig. D b was taken.

(The embryo from which fig. E a was derived had three visceral clefts.)

There have not as yet appeared any connective-tissue cells dorsal to the top of the muscle-plates, so that the posterior nerve-rudiments are still quite free and distinct.

The cells composing them are smaller than the cells of the neural canal; they are round and nucleated; and, indeed, in their histological constitution the nerve-rudiments exhibit no important deviations from the previous stage, and they have hardly increased in size. In their mode of attachment to the neural tube an important change has, however, already commenced to be visible.

In the previous stage the two nerve-rudiments met above the summit of the spinal cord and were broadly attached to it there; now their points of attachment have glided a short distance down the sides of the spinal cord†.

The two nerve-rudiments have therefore ceased to meet above the summit of the canal; and in addition to this they appear in section to narrow very much before becoming united with its walls, so that their junctions with these appear in a transverse section to be effected by at most one or two cells, and are, comparatively speaking, very difficult to observe.

In an embryo but slightly older than that represented in fig. E a the first rudiment of the anterior root becomes visible. This appears, precisely as in *Torpedo*, in the form of a small projection from the ventral corner of the spinal cord (fig. E b, *ar*).

The second step in this stage (Plate 17. fig. F) is comparable, as far as the connective-tissue is concerned, with the section of *Torpedo* (Plate 16. fig. D d). The notochord (the

* This commissure is not satisfactorily represented in the figure. *Vide* Explanation of Plate 18.

† [May 18, 1876.—Observations I have recently made upon the development of the cranial nerves incline me to adopt an explanation of the change which takes place in point of attachment of the spinal nerves to the cord differing from that enunciated in the text. I look upon this change as being apparent rather than real, and as due to a growth of the roof of the neural canal in the median dorsal line, which tends to separate the roots of the two sides more and more, and cause them to assume a more ventral position.]

histological details of whose structure are not inserted in this figure) is rather more developed, and the segmental duct, as was the case with the corresponding *Torpedo*-embryo, has become hollow at its anterior extremity.

The embryo from which the section was taken possessed five visceral clefts, but no trace of external gills.

In the section represented, though from a posterior part of the body, the dorsal nerve-rudiments have become considerably larger than in the last embryo; they now extend beyond the base of the neural canal. They are surrounded to a great extent by mesoblastic tissue, which, as in the case of the *Torpedo*, takes its origin from two sources, (1) from the commencing vertebral bodies, (2) from the summits of the muscle-plates.

It is in many cases very difficult, especially with chromic-acid specimens, to determine with certainty the limits of the rudiments of the posterior root.

In the best specimens a distinct bordering line can be seen, and it is, as a rule, possible to state the characters by which the cells of the nerve-rudiments and vertebral bodies differ. The more important of these are the following:—(1) The cells of the nerve-rudiment are distinctly smaller than those of the vertebral rudiment; (2) the cells of the nerve-rudiment are elongated, and have their long axis arranged parallel to the long axis of the nerve-rudiment, while the cells surrounding them are much more nearly circular.

The cells of the nerve-rudiment measure about $\frac{1}{1600} \times \frac{1}{4500}$ to $\frac{1}{1600} \times \frac{1}{3200}$ inch, those of the vertebral rudiment $\frac{1}{1600} \times \frac{1}{1900}$ inch. The greater difficulty experienced in distinguishing the nerve-rudiment from the connective-tissue in *Pristiurus* than in *Torpedo* arises from the fact that the connective-tissue is much looser and less condensed in the latter than in the former.

The connective-tissue cells which have grown out from the muscle-plates form a continuous arch over the dorsal surface of the neural tube (*vide* Plate 17. fig. F); and in some specimens it is difficult to see whether the arch is formed by the rudiment of the posterior root or by connective-tissue. It is, however, quite easy with the best specimens to satisfy one's self that it is from the connective-tissue, and not the nerve-rudiment, that the dorsal investment of the neural canal is derived.

As in the previous case, the upper ends of each pair of posterior nerve-rudiments are quite separate from one another, and appear in sections to be united by a very narrow root to the walls of the neural canal at the position indicated in fig. F*.

The cells forming the nerve-rudiments have undergone slight modifications; they are for the most part more distinctly elongated than in the earlier stage, and appear slightly smaller in comparison with the cells of the neural canal.

They possess as yet no distinctive characters of nerve-cells. They stain more deeply with osmic acid than the cells around them, but with hæmatoxylin there is but a very slight difference in intensity between their colouring and that of the neighbouring connective-tissue cells.

* The artist has not been very successful in rendering this figure.

The anterior roots have grown considerably in length, but their observation is involved in the same difficulties with chromic-acid specimens as that of the posterior rudiments.

There is a further difficulty in observing the anterior roots, which arises from the commencing formation of white matter in the cord. This is present in all the anterior sections of the embryo from which fig. F is taken. When the white matter is formed the cells constituting the junction of the anterior nerve-root with the spinal cord undergo the same changes as the cells which are being converted into the white matter of the cord, and become converted into nerve-fibres; these do not stain with hæmatoxylin, and thus an apparent space is left between the nerve-root and the spinal cord. This space by careful examination may be seen to be filled up with fibres. In osmic-acid sections, although even in these the white matter is stained less deeply than the other tissues, it is a matter of comparative ease to observe the junction between the anterior nerve-root and the spinal cord.

I have been successful in preparing satisfactory longitudinal sections of embryos somewhat older than that shown in fig. F, and they bring to light several important points in reference to the development of the spinal nerves. Three of these sections are represented in Plate 17. figs. G 1, G 2, & G 3.

The sections are approximately horizontal and longitudinal. G 1 is the most dorsal of the three; it is not quite horizontal though nearly longitudinal. The section passes exactly through the point of attachment of the posterior roots to the walls of the neural canal.

The posterior rudiments appear as slight prominences of rounded cells projecting from the wall of the neural canal. From transverse sections the attachment of the nerves to the wall of the neural canal is proved to be very narrow, and from these sections it appears to be of some length in the direction of the long axis of the embryo. A combination of the sections taken in the two directions leads to the conclusion that the nerves at this stage thin out like a wedge before joining the spinal cord.

The independent junctions of the posterior rudiments with the spinal cord at this stage are very clearly shown, though the rudiments are probably united with each other just dorsal to their junction with the spinal cord.

The nerves correspond in number with the muscle-plates, and each arises from the spinal cord, nearly opposite the middle line of the corresponding muscle-plates (figs. G 1 & G 2).

Each nerve-rudiment is surrounded by connective-tissue cells, and is separated from its neighbours by a considerable interval.

At its origin each nerve-rudiment lies opposite the median portion of a muscle-plate (figs. G 1 & G 2); but, owing to the muscle-plate acquiring an oblique direction, at the level of the dorsal surface of the notochord it appears in horizontal sections more nearly opposite the interval between two muscle-plates (figs. G 2 & G 3).

In horizontal sections I find masses of cells which make their appearance on a level with the ventral surface of the spinal cord. I believe I have in some sections successfully traced these into the spinal cord, and I have little doubt that they are the

anterior roots of the spinal nerves; they are opposite the median line of the muscle-plates, and do not appear to join the posterior roots (*vide* fig. G 3, *ar*).

At the end of this period or second stage the main characters of the spinal nerves in *Pristiurus* are the following:—

(1) The posterior nerve-rudiments form somewhat wedge-shaped masses of tissue attached dorsally to the spinal cord.

(2) The cells of which they are composed are typical undifferentiated embryonic cells, which can hardly be distinguished from the connective-tissue cells around them.

(3) The nerves of each pair no longer meet above the summit of the spinal canal, but are independently attached to its sides.

(4) Their dorsal extremities are probably united by commissures.

(5) The anterior roots have appeared; they form small conical projections from the ventral corner of the spinal cord, but have no connexion with the posterior rudiments.

The Third Stage of the Spinal Nerves in Pristiurus.

With the *third stage* the first distinct histological differentiations of the nerve-rudiments commence. Owing to the changes both in the nerves themselves and in the connective-tissue around them, which becomes less compact and its cells stellate, the difficulty of distinguishing the nerves from the surrounding cells vanishes; and the difficulties of investigation in the later stages are confined to the modes of attachment of the nerves to the neural canal, and the histological changes which take place in the rudiments themselves.

The stage may be considered to commence at the period when the external gills first make their appearance as small buds from the walls of the visceral clefts. Already, in the earliest rudiments of the posterior root of this period now figured, a number of distinct parts are visible (Plate 17. fig. H 1).

Surrounding nearly the whole structure there is present a delicate investment similar to that which I mentioned as surrounding the neural canal and other organs; it is quite structureless, but becomes coloured with all staining reagents. I must again leave open the question whether it is to be looked upon as a layer of coagulated protoplasm or as a more definite structure. This investment completely surrounds the proximal portion of the posterior root, but vanishes near its distal extremity.

The nerve-rudiment itself may be divided into three distinct portions:—(1) the proximal portion, in which is situated the pedicle of attachment to the wall of the neural canal; (2) an enlarged portion, which may conveniently, from its future fate, be called the ganglion; (3) a distal portion beyond this. The proximal portion presents a fairly uniform diameter, and ends dorsally in a rounded expansion; it is attached remarkably enough, not by its extremity, but by its side, to the spinal cord. The dorsal extremities of the posterior nerves are therefore free; as was before mentioned, they probably serve as the starting-point of the longitudinal commissures between the posterior roots.

The spinal cord at this stage is still made up of fairly uniform cells, which do not

differ in any important particulars from the cells which composed it during the last stage. The outer portion of the most peripheral layer of cells has already begun to be converted into the white matter.

The delicate investment spoken of before still surrounds the whole spinal cord, except at the points of junction of the cord with the nerve-rudiments. Externally to this investment, and separated from it for the most part by a considerable interval, a mesoblastic sheath (Plate 17. fig. H 1, *i*) for the spinal cord is beginning to be formed.

The attachment of the nerve-rudiments to the spinal cord, on account of its smallness, is still very difficult to observe. In many specimens where the nerve is visible a small prominence may be seen rising up from the spinal cord at a point corresponding to *x* (Plate 17. fig. H 1). It is, however, rare to see this prominence and the nerve continuous with each other: as a rule they are separated by a slight space, and frequently one of the cells of the mesoblastic investment of the spinal cord is interposed between the two. In some especially favourable specimens, similar to the one figured, there can be seen a distinct cellular prominence (fig. H 1, *x*) from the spinal cord, which becomes continuous with a small prominence on the lateral border of the nerve-rudiment near its free extremity. The absence of a junction between the two in a majority of sections is only what might be expected, considering how minute the junction is.

Owing to the presence of the commissure connecting the posterior roots, some part of a nerve is present in every section.

The proximal extremity of the nerve-rudiment itself is composed of cells, which, by their smaller size and a more circular form, are easily distinguished from cells forming the ganglionic portion of the nerve.

The ganglionic portion of the nerve, by its externally swollen configuration, is at once recognizable in all the sections in which the nerve is complete. The delicate investment before mentioned is continuous around it. The cells forming it are larger and more elongated than the cells forming the upper portion of the nerve-rudiment: each of them possesses a large and distinct nucleus.

The remainder of the nerve-rudiment forms the commencement of the true nerve. It can in this stage be traced only for a very small distance, and gradually fades away, in such a manner that its absolute termination is very difficult to observe.

The connective-tissue cells which surround the nerve-rudiment are far looser than in the last stage, and are commencing to throw out processes and become branched.

The anterior root-nerve has grown very considerable since the last stage. It projects from the same region of the cord as before, but on approaching the muscle-plate takes a sudden bend downwards (fig. H II, *ar*).

I have failed to prove that the anterior and posterior roots are at this stage united.

Fourth Stage.

In an embryo but slightly more advanced than the one last described, important steps have been made in the development of the nerve-rudiment. The spinal cord itself now

possesses a covering of white matter; this is thickest at the ventral portion of the cord, and extends to the region of the posterior root of the spinal nerve.

The junction of the posterior root with the spinal cord is easier to observe than in the last stage.

It is still effected by means of unaltered cells, though the cells which form the projection from the cord to the nerve are commencing to undergo changes similar to those of the cells which are being converted into white matter.

In the rudiment of the posterior root itself there are still three distinct parts, though their arrangement has undergone some alteration and their distinctness has become more marked (Plate 17. fig. I 1).

The root of the nerve (fig. I 1, *pr*) consists, as before, of nearly circular cells, each containing a nucleus, very large in proportion to the size of the cell. The cells have a diameter of about $\frac{1}{3000}$ of an inch. This mass forms not only the junction between the ganglion and the spinal canal, but is also continued into a layer investing the outer side of the ganglion and continuous with the nerve beyond the ganglion.

The cells which compose the ganglion (fig. I 1, *sp.g*) are easily distinguished from those of the root. Each cell is elongated with an oval nucleus, large in proportion to the cell; and its protoplasm appears to be continued into an angular, not to say fibrous process, sometimes at one and more rarely at both ends. The processes of the cells are at this stage very difficult to observe: figs. I a, I b, I c represent three cells provided with them and placed in the positions they occupied in the ganglion.

The relatively very small amount of protoplasm in comparison to the nucleus is fairly represented in these figures, though not in the drawing of the ganglion as a whole. In the centre of each nucleus is a nucleolus.

Fig. I b, in which the process points towards the root of the nerve, I regard as a commencing nerve-fibre: its more elongated shape seems to imply this. In the next stage special bundles of nerve-fibres become very conspicuous in the ganglion. The long diameter of an average ganglion-cell is about $\frac{1}{1000}$ of an inch. The whole ganglion forms an oval mass, well separated both from the nerve-root and the nerve, and is not markedly continuous with either. On its outer side lies the downward process of the nerve-root before mentioned.

The nerve itself is still, as in the last case, composed of cells which are larger and more elongated than either the cells of the root or the ganglion.

The condition of the anterior root at this stage is hardly altered from what it was; it is composed of very small cells, which with hæmatoxylin stain more deeply than any other cell of the section. A figure of it is given in I II.

Horizontal longitudinal sections of this stage are both easy to make and very instructive. On Plate 18. fig. K 1 is represented a horizontal section through a plane near the dorsal surface of the spinal cord: each posterior root is seen in this section to lie nearly opposite the anterior extremity of a muscle-plate.

In a more ventral plane (fig. K II) this relation is altered, and the posterior roots lie opposite the hinder parts of the muscle-plates.

The nerves themselves are invested by the hyaline membrane spoken of above; and surrounding this again there is present a delicate mesoblastic investment of spindle-shaped cells.

Longitudinal sections also throw light upon the constitution of the anterior nerve-roots (*vide* fig. K II, *ar*). In the two segments on the left-hand side in this figure the anterior roots are cut through as they are proceeding, in a more or less horizontal course, from the spinal cord to the muscle-plates.

Where the section (which is not quite horizontal) passes through the plane of the notochord, as on the right-hand side, the anterior roots are cut transversely. Each root, in fact, changes its direction, and takes a downward course.

The anterior roots are situated nearly opposite the middle of the muscle-plates: their section is much smaller than that of the posterior roots, and with hæmatoxylin they stain more deeply than any of the other cells in the preparation.

The anterior roots, so far as I have been able to observe, do not at this stage unite with the posterior; but on this point I do not speak with any confidence.

The period now arrived at forms a convenient break in the development of the spinal nerves; and I hope to treat the remainder of the subject, especially the changes in the ganglion, the development of the ganglion-cells, and of the nerve-fibres, in a subsequent paper.

I will only add that, not long after the stage last described, the posterior root unites with the anterior root at a considerable distance below the cord: this is shown in Plate 18. fig. L. Still later the portion of the root between the ganglion and the spinal cord becomes converted into nerve-fibres, and the ganglion becomes still further removed from the cord, while at the same time it appears distinctly divided into two parts.

As regards the development of the cranial nerves, I have made a few observations, which, though confessedly incomplete, I would desire to mention here, because, imperfect as they are, they seem to show that in Elasmobranch Fishes the cranial nerves resemble the spinal nerves in arising as outgrowths from the central nervous system.

I have given a figure of the development of a posterior root of a cranial nerve in fig. M I. The section is taken from the same embryo as figs. B I, B II, and B III.

It passes through the anterior portion of a thickening of the external epiblast, which eventually becomes involuted as the auditory vesicle.

The posterior root of a nerve (VII) is seen growing out from the summit of the hind brain in precisely the same manner that the posterior roots of the spinal nerves grow out from the spinal cord: it is the rudiment of the seventh or facial nerve. The section behind this (fig. M II), still in the region of the ear, has no trace of a nerve, and thus serves to show the early discontinuity of the posterior nerve-rudiments which arise from the brain.

I have as yet failed to detect any cranial anterior roots like those of the spinal nerves*. The similarity in development between the cranial and spinal nerves is especially interesting, as forming an important addition to the evidence which at present exists that the cranial nerves are only to be looked on as spinal nerves, especially modified in connexion with the changes which the anterior extremity of the body has undergone in existing vertebrates.

My results may be summarized as follows:—

Along the extreme dorsal summit of the spinal cord there arises on each side a continuous outgrowth.

From each outgrowth processes corresponding in number to the muscle-plates grow downwards. These are the posterior nerve-rudiments.

The outgrowths, at first attached to the spinal cord throughout their whole length, soon cease to be so, and remain in connexion with it in certain spots only, which form the junction of the posterior roots with the spinal cords.

The original outgrowth on each side remains as a bridge, uniting together the dorsal extremities of all the posterior rudiments. The points of junction of the posterior roots with the spinal cord are at first situated at the extreme dorsal summit of the latter, but eventually travel down, and are finally placed on the sides of the cord.

After these events the posterior nerve-rudiments grow rapidly in size, and become differentiated into a root (by which they are attached to the spinal canal), a ganglion, and a nerve.

The anterior roots, like the posterior, are outgrowths from the spinal cord; but the outgrowths to form them are from the first discontinuous, and the points from which they originally spring remain as those by which they are permanently attached to the spinal cord, and do not, as in the case of the posterior roots, undergo a change of position. The anterior roots arise, not vertically below, but opposite the intervals between the posterior roots.

The anterior roots are at first quite separate from the posterior roots; but soon after the differentiation of the posterior rudiment into a root, ganglion, and nerve a junction is effected between each posterior nerve and the corresponding anterior root. The junction is from the first at some little distance from the ganglion.

Investigators have hitherto described the spinal nerves as formed from part of the mesoblast of the protovertebræ. His alone, so far as I know, takes a different view.

His's† observations lead him to the conclusion that the posterior roots are developed as ingrowths from the external epiblast into the space between the protovertebræ and the neural canal. These subsequently become constricted off, unite with the neural canal and form spinal nerves.

* [May 18, 1876.—Subsequent observations have led me to the conclusion that no anterior nerve-roots are to be found in the brain.]

† Erste Anlage des Wirbelthier-Leibes.

These statements, which have not been since confirmed, diverge nearly to the same extent from my own results as does the ordinary account of the development of these parts.

Hensen (Virchow's 'Archiv,' vol. xxxi. 1864) also looks upon the spinal nerves as developed from the epiblast, but not as a direct result of his own observations*.

Without attempting, for the present at least, to explain this divergence, I venture to think that the facts which I have just described have distinct bearings upon one or two important problems.

One point of general anatomy upon which they throw considerable light is the primitive origin of nerves.

So long as it was admitted that the spinal and cerebral nerves developed in the embryo independently of the central nervous system, their mode of origin always presented to my mind considerable difficulties.

It never appeared clear how it was possible for a state of things to have arisen in which the central nervous system, as well as the peripheral terminations of nerves, whether motor or sensory, were formed independently of each other, while between them a third structure was developed which, growing in both directions (towards the centre and towards the periphery), ultimately brought the two into connexion.

That such a condition could be a primitive one seemed scarcely possible.

Still more remarkable did it appear, on the supposition that the primitive mode of formation of these parts was represented in the developmental history of vertebrates, that we should find similar structural elements in the central and in the peripheral nervous systems.

The central nervous system arises from the epiblast, and yet contains precisely similar nerve-cells and nerve-fibres to the peripheral nervous system, which, if derived, as is usually stated, from the mesoblast, was necessarily supposed to have a completely different origin from the central nervous system.

Both of these difficulties are to a great extent removed by the facts of the development of these parts in Elasmobranchs.

If it be admitted that the spinal roots develop as outgrowths from the central nervous system in Elasmobranch Fishes, the question arises, how far it can be supposed to be possible that in other vertebrates the spinal roots and ganglia develop independently of the spinal cord, and only subsequently become united with it.

I have already insisted that this cannot be the primary condition; and though I am of opinion that the origin of the nerves in higher vertebrates ought to be worked over again, yet I do not think it impossible that, by a secondary adaptation, the nerve-roots might develop in the mesoblast†.

* [May 18, 1876.—Since the above was written Hensen has succeeded in showing that in mammals the rudiments of the posterior roots arise in a manner closely resembling that described in the present paper; and I have myself, within the last few days, made observations which incline me to believe that the same holds good for the chick. My observations are as yet very incomplete.]

† [May 18, 1876.—Hensen's observations, as well as those recently made by myself on the chick, render it almost certain that the nerves in all Vertebrates spring from the spinal cord.]

The presence of transverse commissures connecting the central ends of all the posterior roots is very peculiar. The commissures may possibly be looked on as outlying portions of the cord, rather than as parts of the nerves.

I have not up to this time followed their history beyond a somewhat early period in embryonic life, and am therefore unacquainted with their fate in the adult.

As far as I am aware, no trace of similar structures has been met with in other vertebrates.

The commissures have a very strong resemblance to those by which in Elasmobranch Fishes the glossopharyngeal nerve and the branches of the pneumogastric are united in an early embryonic stage*.

I think it not impossible that the commissures in the two cases represent the same structures. If this is the case, it would seem that the junction of a number of nerves to form the pneumogastric is not a secondary state, but the remnant of a primary one, in which all the spinal nerves were united, as they embryonically are in Elasmobranchs.

One point brought out in my investigations appears to me to have bearings upon the origin of the central canal of the Vertebrate nervous system, and in consequence upon the origin of the Vertebrate group itself.

The point I allude to is the posterior nerve-rudiments making their first appearance at the *extreme dorsal summit* of the spinal cord.

The transverse section of the ventral nervous cord of an ordinary segmented worm consists of two symmetrical halves placed side by side.

If by a mechanical folding the two lateral halves of the nervous cord became bent towards each other, while into the groove formed between the two the external skin became pushed, we should have an approximation to the Vertebrate spinal cord. Such a folding might take place to give extra rigidity to the body in the absence of a vertebral column.

If this folding were then completed in such a way that the groove, lined by external skin and situated between the two lateral columns of the nervous system, became converted into a canal, above and below which the two columns of the nervous system united, we should have in the transformed nervous cord an organ strongly resembling the spinal cord of Vertebrates.

This resemblance would even extend beyond mere external form. Let the ventral nervous cord of the common earthworm, *Lumbricus agricola*, be used for comparison †, a transverse section of which is represented by Leydig‡ and Claparède. In this we find that on the ventral surface (the Annelidan ventral surface) of the nervous cord the ganglion-cells (grey matter) (*k*) are situated, and on the dorsal side the nerve-fibres or

* Balfour, "A Preliminary Account of the Development of Elasmobranch Fishes," Q. J. Micros. Sc. 1874, plate xv. fig. 14, *v.g.*

† The nervous cords of other Annelids resemble that of *Lumbricus* in the relations of the ganglion-cells of the nerve-fibres.

‡ Tafeln zur vergleichenden Anatomie, Taf. iii. fig. 8.

white matter (*h*). If the folding that I have supposed were to take place, the grey and white matters would have very nearly the relative situations which they have in the Vertebrate spinal cord.

The grey matter would be situated in the interior and surround the epithelium of the central canal, and the white matter would nearly surround the grey and form the anterior white commissure. The nerves would then arise, not from the sides of the nervous cord as in existing Vertebrates, but from its extreme ventral summit.

One of the most striking features which I have brought to light with reference to the development of the posterior roots, is the fact of their growing out from the extreme dorsal summit of the neural canal—a position analogous to the ventral summit of the Annelidan nervous cord. Thus the posterior roots of the nerves in Elasmobranchs arise in the exact manner which might have been anticipated were the spinal cord due to such a folding as I have suggested. The argument from the nerves becomes the stronger, from the great peculiarity in the position of the outgrowth, a feature which would be most perplexing without some such explanation as I have proposed. The central epithelium of the neural canal according to this view represents the external skin; and its ciliation is to be explained as a remnant of the ciliation of the external skin now found amongst many of the lower Annelids.

I have, however, employed the comparison of the Vertebrate and Annelidan nervous cords, not so much to prove a genetic relation between the two as to show the *à priori* possibility of the formation of a *spinal canal* and the *à posteriori* evidence we have of the Vertebrate spinal canal having been formed in the way indicated.

I have not made use of what is really the strongest argument for my view, viz. that the embryonic mode of formation of the spinal canal, by a folding in of the external epiblast, is the very method by which I have supposed the spinal canal to have been formed in the ancestors of Vertebrates.

My object has been to suggest a meaning for the peculiar primitive position of the posterior roots, rather than to attempt to explain in full the origin of the spinal canal.

Explanation of the Plates*.

PLATE 16.

Fig. A. Section through the dorsal region of an embryo of *Scyllium stellare*, with the rudiments of two visceral clefts. The section illustrates the general features at a period anterior to the appearance of the posterior nerve-roots.

nc, neural canal; *mp*, muscle-plate; *ch*, notochord; *x*, subnotochordal

* The figures on these Plates give a fair general idea of the appearance presented by the developing spinal nerves; but the finer details of the original drawings have in several cases become lost in the process of copying.

The figures which are tinted represent sections of embryos hardened in osmic acid; those without colour sections of embryos hardened in chromic acid.

rod; *ao*, rudiment of dorsal aorta; *so*, somatopleure; *sp*, splanchnopleure; *al*, alimentary tract. All the parts of the section except the spinal cord are drawn somewhat diagrammatically.

Figs. B I, B II, B III. Three sections of a *Pristiurus*-embryo. B I is through the heart, B II through the anterior part of the dorsal region, and B III through a point slightly behind this. Drawn with a camera. (Zeiss CC ocul. 2.)

In B III there is visible a slight proliferation of cells from the dorsal summit of the neural canal.

In B II this proliferation definitely constitutes two club-shaped masses of cells (*pr*), both attached to the dorsal summit of the neural canal. The masses are the rudiments of the posterior nerve-roots.

In B I the rudiments of the posterior roots are of considerable length.

pr, rudiment of posterior roots; *nc*, neural canal; *mp*, muscle-plate; *ch*, notochord; *x*, subnotochordal rod; *ao*, dorsal aorta; *so*, somatopleure; *sp*, splanchnopleure; *al*, alimentary canal; *ht*, heart.

Fig. C. Section from a *Pristiurus*-embryo, slightly older than B. Camera. (Zeiss CC ocul. 2.) The embryo from which this figure was taken was slightly distorted in the process of removal from the blastoderm.

vr, rudiment of vertebral body. Other reference letters as in previous figures.

Fig. D a. Section through the dorsal region of a *Torpedo*-embryo with three visceral clefts. (Zeiss CC ocul. 2.) The section shows the formation of the dorsal nerve-rudiments (*pr*) and of a ventral anterior nerve-rudiment (*ar*), which at this early stage is not distinctly cellular.

ar, rudiment of an anterior nerve-root; *y*, cells left behind on the separation of the external skin from the spinal cord; *c*, connective-tissue cells springing from the summit of the muscle-plates. Other reference letters as above.

Fig. D b. Section from dorsal region of a *Torpedo*-embryo somewhat older than D a. Camera. (Zeiss CC ocul. 2.) The posterior nerve-rudiment is considerably longer than in fig. D a, and its pedicle of attachment to the spinal cord is thinner. The anterior nerve-rudiment, of which only the edge is present in the section, is distinctly cellular.

m, mesoblast growing up from vertebral rudiment; *sd*, segmental duct.

Fig. D c. Section from a still older *Torpedo*-embryo. Camera. (Zeiss CC ocul. 2.) The connective-tissue cells are omitted. The rudiment of the ganglion (*g*) on the posterior root has appeared. The rudiment of the posterior nerve is much longer than before, and its junction with the spinal cord is difficult to detect. The anterior root is now an elongated cellular structure.

g, ganglion.

Fig. D d. Longitudinal and vertical section through a *Torpedo*-embryo of the same age as D c.

The section shows the commissures uniting the posterior roots.

PLATE 17.

Fig. E a. Section of a *Pristiurus*-embryo belonging to the second stage. Camera. (Zeiss CC ocul. 2.) The section shows the constriction of the pedicle which attaches the posterior nerve-rudiments to the spinal cord.

pr, rudiment of posterior nerve-root; *nc*, neural canal; *mp*, muscle-plate; *vr*, vertebral rudiment; *sd*, segmental duct; *ch*, notochord; *so*, somatopleure; *sp*, splanchnopleure; *ao*, aorta; *al*, alimentary canal.

Fig. E b. Section of a *Pristiurus*-embryo slightly older than E a. Camera. (Zeiss CC ocul. 2.) The section shows the formation of the anterior nerve-root (*ar*).

ar, rudiment of the anterior nerve-root.

Fig. F. Section of a *Pristiurus*-embryo with the rudiments of five visceral clefts. Camera. (Zeiss CC ocul. 2.)

The rudiment of the posterior root is seen surrounded by connective-tissue, from which it cannot easily be distinguished. The artist has not been very successful in rendering this figure.

Figs. G 1, G 2, G 3. The longitudinal and horizontal section of an embryo somewhat older than F. The embryo from which these sections were taken was hardened in osmic acid, but the sections have been represented without tinting. G 1 is most dorsal of the three sections. Camera. (Zeiss CC ocul. 1.)

nc, neural canal; *sp.c*, spinal cord; *pr*, rudiment of posterior root; *ar*, rudiment of anterior root; *mp*, muscle-plate; *c*, connective-tissue cells; *ch*, notochord.

Fig. H I. Section through the dorsal region of a *Pristiurus*-embryo in which the rudimentary external gills are present as very small knobs. Camera. (Zeiss CC ocul. 2.)

The section shows the commencing differentiation of the posterior nerve-rudiment into root (*pr*), ganglion (*sp.g*), and nerve (*n*), and also the attachment of the nerve-root to the spinal cord (*x*). The variations in the size and shape of the cells in the different parts of the nerve-rudiment are completely lost in the figure.

pr, posterior nerve-root; *sp.g*, ganglion of posterior root; *n*, nerve of posterior root; *x*, attachment of posterior root to spinal cord; *w*, white matter of spinal cord; *i*, mesoblastic investment to the spinal cord.

Fig. H II. Section through the same embryo as H I. (Zeiss CC ocul. 1.)

The section contains an anterior root, which takes its origin at a point opposite the interval between two posterior roots.

The white matter has not been very satisfactorily represented by the artist.

Figs. I I, I II. Two sections of a *Pristiurus*-embryo somewhat older than H. Camera. (Zeiss CC ocul. 1.)

The connective-tissue cells are omitted.

Figs. I a, I b, I c. Three isolated cells from the ganglion of one of the posterior roots of the same embryo.

PLATE 18.

Figs. K I, K II. Two horizontal longitudinal sections through an embryo in which the external gills have just appeared. K I is the most dorsal of the two sections. Camera. (Zeiss CC ocul. 1.)

The sections show the relative positions of the anterior and posterior roots at different levels.

pr, posterior nerve-rudiment; *ar*, anterior nerve-rudiment; *sp.c*, spinal cord; *n.c*, neural canal; *mp*, muscle-plate; *mp'*, first-formed muscles.

Fig. L. Longitudinal and vertical section through the trunk of a *Scyllium*-embryo after the external gills have attained their full development. Camera. (Zeiss CC ocul. 1.)

The embryo was hardened in a mixture of chromic acid and osmic acid.

The section shows the commissures which dorsally unite the posterior roots, and also the junction of the anterior and posterior roots. The commissures are unfortunately not represented in the figure with great accuracy; their outlines are in nature perfectly regular, and not, as in the figure, notched at the junctions of the cells composing them. Their cells are apparently more or less completely fused, and certainly not nearly so clearly marked as in the figure. The commissures stain very deeply with the mixture of osmic and chromic acid, and form one of the most conspicuous features in successful longitudinal sections of embryos so hardened. In sections hardened with chromic acid only they cannot be seen with the same facility.

sp.c, spinal cord; *gr*, grey matter; *w*, white matter; *ar*, anterior root; *pr*, posterior root; *x*, commissure uniting the posterior roots.

Figs. M I, M II. Two sections through the head of the same embryo as fig. B. M I, the foremost of the two, passes through the anterior part of the thickening of epiblast, which becomes involuted as the auditory vesicle. It contains the rudiment of the seventh nerve, VII. Camera. (Zeiss CC ocul. 2.)

VII, rudiment of seventh nerve; *au*, thickening of external epiblast, which becomes involuted as the auditory vesicle; *n.c*, neural canal; *ch*, notochord; *pp*, body-cavity in the head; *so*, somatopleure; *sp*, splanchnopleure; *al*, throat, exhibiting an outgrowth to form the first visceral cleft.

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VIII. *On the Fossil Mammals of Australia.*—Part X. Family Macropodidæ: *Mandibular Dentition and Parts of the Skeleton of* Palorchestes; *additional evidences of* Macropus Titan, Sthenurus, *and* Procoptodon. *By Professor* Owen, *C.B., F.R.S., &c.*

Received May 10, 1875,—Read June 10, 1875.

§ 1. *Introduction.*—The evidences of these extinct Mammals which have been made known through the 'Transactions' of the Royal Society have stimulated the search and transmission of additional fossils, from which are selected for the present communication those tending to complete the restoration of the gigantic kind of Kangaroo indicated by the portion of skull described and figured in the volume for 1874*, and others adding to the knowledge of the dental system and osteology of *Sthenurus*, *Procoptodon*, and *Macropus Titan*.

To E. S. Hill, Esq., of Woollahra, Sydney, I am indebted, through his brother-in-law Sir Daniel Cooper, Bart., for the portions of mandible adding to the dental characters of *Palorchestes*; and to George Frederic Bennett, Esq., of Darling Downs, Queensland, I chiefly owe, through his father Dr. Bennett, F.L.S., of Sydney, the parts of the skeleton of the same extinct species about to be described, and the remaining subjects of the present paper.

§ 2. *Palorchestes Azael* (Mandibular Characters and Dentition).—So much of the dental characters of the genus and species as could be defined from the condition of the maxillary teeth, described and figured in the above-cited volume, concurred with the cranial characters in showing that such large extinct Kangaroo deviated less from the type of the existing bilophodont *Macropodidæ* than did the species of the genus *Procoptodon*, some of which (*Proc. Goliah*, for example†) rivalled *Palorchestes* in bulk.

This conclusion is sustained by the evidence afforded by the subjects of Plate 19.

The chief of these is a portion of the right mandibular ramus (fig. 1) with the teeth symbolized as d_4, m_1, m_2, and part of m_3. A smaller portion of the left ramus of the same jaw (ib. fig. 5) contained the molar (m_1) entire, a portion of m_2, and the sockets of the teeth (d_4 and p_3).

The depth of the ramus at the interval between p_3 and d_4 is 3 inches 3 lines; at the socket of the last molar (m_3) it is 2 inches 8 lines. Such gain of depth as the

* Phil. Trans. 1874, p. 797, plates lxxxi.–lxxxiii.

† *Tom. cit.* p. 791, plates lxxix., lxxx.

mandible extends from the back to the front of the molar series is a character of the lower jaw of *Macropus**, which contrasts with the uniformity of depth in that of *Sthenurus*† and *Protemnodon*‡.

The socket of the premolar (ib. fig. 5, p_3) shows the two roots of that tooth to have been simple; the hinder one, in section circular, with a diameter of 3 lines, was larger than the fore root, which was compressed and elliptic in section. The fore-and-aft length of the crown of this tooth is indicated to have been between 8 and 9 lines. This accords with the same admeasurement of the upper premolar (p_3) of the fossil from another and remote locality, figured in plate lxxxii. of the Phil. Trans. *tom. cit.*

The fore root of the next molar in the mandibular fossil from Darling Downs (Plate 19. fig. 5, d_4) is transversely elliptic, 5 lines in long diameter, with a mid groove along its hind surface. The hind root, with a larger and deeper longitudinal groove on its fore surface, is also transversely elliptical, with a long diameter of $6\frac{1}{2}$ lines. The crown of this tooth, preserved in the right ramus (ib. figs. 1 & 2, d_4), shows a low, short prebasal ridge (f), upon which the exposed dentine is continuous with that of the much-worn surface of the fore lobe (a), indicative of a linked connexion therewith. Along the mid link (r), also, a linear tract of dentine extends to the hind lobe (b). The postbasal ridge is feebly indicated at this stage of wear by a narrow fold of enamel, which extends from the dentinal tract at the back of the grinding-surface of the hind lobe, downward and outward to near the base of the crown. The fore-and-aft diameter of d_4 is $10\frac{1}{2}$ lines (23 millims.), the transverse diameter of the hind lobe is $7\frac{1}{2}$ lines (15 millims.).

The chief difference in size of d_4 in the upper jaw§ is in the greater proportional breadth of the crown—a characteristic of the upper molars in *Macropodidæ*: so much as remains of the prebasal ridge and of the two main lobes in the maxillary tooth conforms to the character of the mandibular homotype.

The third molar (m_1) is well preserved in both rami of the present lower jaw. A continuous tract of dentine is exposed, by wear, from the fore lobe along the mid link to the postbasal ridge (g). The prebasal ridge is limited to the inner half of the fore surface of the fore lobe, where, also, it is alone visible in m_1 of the upper jaw. The postbasal ridge (g) is more developed on the inner side of the hind link, where it is divided from the hind lobe by a fossa; on the outer side of the link the ridge rapidly sinks and subsides near the base of the crown; the mid part of the postbasal ridge is half an inch above the basal line of the enamel (fig. 8, g). The main valley expands as it descends from each side of the mid link (r), and is closed by a low bar on both the outer (ib. fig. 6, v) and inner (ib. fig. 7, v') sides of the tooth. The fore-and-aft extent of the mandibular tooth (m_1) is 1 inch, as in its homotype of the upper jaw; the transverse diameter of the hind lobe is 8 lines, in the upper tooth 9 lines.

The less-worn crown of m_2 shows more of the true pattern of the grinding-surface

* See Phil. Trans. 1874, plate xxii. figs. 13, 15.

† Ibid. figs. 5, 6.

‡ *Tom. cit.* plate xxv. figs. 7, 8.

§ *Tom. cit.* plate lxxxii. fig. 1, d_4.

in the lower molars of the present species. The vertical indent (Plate 19. fig. 1, m_2) on the inner fore part of the crown, leading to the better developed inner part of the prebasal ridge, is deeper than in m_1, and causes a concave contour of the anterior enamel-border of the fore lobe.

The mid link projects from the middle of the hind enamel-border of that lobe, touches, but is not continuous with, the hind part of the link sent off from the outer side of the fore part of the hind lobe. The vertical prominence from the corresponding part of the crown of the lower molars in *Nototherium* is the homologue of this part of the mid link in *Palorchestes*.

The inner concave part of the fore surface of the hind lobe shows two fine vertical fissures in m_2. From the low link at the back of the hind lobe the postbasal ridge sinks toward the base, thicker and shorter on the inner than on the outer side. The fore-and-aft extent of m_2 is 1 inch $1\frac{1}{2}$ line (29 millims.); the transverse breadth of the hind lobe is $8\frac{1}{2}$ lines (18 millims.). Here the lower penultimate molar is longer in the first diameter by 1 line than the corresponding tooth above, the breadth being the same.

The breadth of the fore lobe of m_3 (ib. fig. 2) is 9 lines; the length of the crown, if entire, would seem to have been, as in the perfect tooth in figure 4, 1 inch 2 lines, or 1 line longer than the corresponding molar above. The proportions of the upper and lower last two molars in *Macropus Titan* are repeated in *Palorchestes Azael*.

The fracture of the molar (m_3, *in situ*) in figs. 1 & 2 shows the continuous part of the mid link to be 3 lines in vertical extent, the whole height of the link being 5 lines where it rises from the valley (fig. 3, *r*). The exposed hind root of this molar curves outward as it descends, and is bifurcated at the extremity. Beneath it the fracture shows the dental canal (fig. 3). The inner bar in m_3, as in m_2, is feebly marked at the inner entry of the valley (fig. 4).

The enamel near the base of the crown and at parts of the outer surface shows, as in the upper molars, the fine rugæ and punctations like those in the molars of *Nototherium* and *Diprotodon*; and the generic pattern of the molars of *Palorchestes* among the *Macropodidæ* indicates a transitional condition between the Kangaroos and those more gigantic extinct Marsupials.

The outer surface of the mandibular ramus of the species, for which grounds are above assigned to justify its reference to *Palorchestes Azael*, shows a vascular or nervous outlet some way below the interval between m_1 and m_2; but this may be an individual and inconstant character.

The depth of the horizontal ramus being given in fig. 1, I have restored the entire skull in outline (Plate 20), with a finished view of the left side of the original and still unique fossil, not figured in my former Memoir.

§ 3. *Palorchestes* (Sacrum).—From the same formation in Darling Downs, Queensland, I have received portions of the pelvis and of the hind limbs with macropodal characters, and of a size corresponding with that of the above-described portions of mandible.

The sacrum (Plate 21. fig. 1) consists of two vertebræ with the characters of those of *Macropus rufus**, but with a difference of size shown in the following admeasurements:—

	Macropus rufus. in. lines.	*Palorchestes*. in. lines.
Length of sacrum (at zygapophyses)	3 2	4 10
Breadth of sacrum (across fore part)	3 5	5 6
Breadth of centrum of first vertebra	1 7	2 6

The Kangaroo yielding the recent bone compared was the largest example seen by Mr. Gould in his travels in Australia†, and no specimen of *Macropus major* has yet been recorded of superior size.

The comparatively gigantic leaper yielding the fossil seems to have been an aged individual, for so much anchylosis has taken place between the second sacral (c 2) and first caudal (cd 1) as to have kept those vertebræ in natural connexion during the period of petrifaction.

The transverse processes of the second sacral take a greater relative share in the formation of the sacro-iliac symphysis in *Palorchestes* than in the above-named recent species, and the shape is rather more subquadrate than triangular. The joint between the first and second sacral is not obliterated. The intervertebral foramina (ib. *i*, *i*) are rather smaller, relatively, than in *Macropus rufus*, and suggest that the hind limb may not have predominated over the fore limb in so great a degree in the larger and heavier Kangaroo. The pair of ridges on the hæmal surface of the centrum of the second sacral (ib. *k*, *k*) are better marked in the fossil. In this the neural arch of the first sacral has been broken away.

The first caudal vertebra of *Palorchestes* (ib. figs. 2, 3) is 2 inches 11 lines in length, 1 inch 6 lines across the hinder articular end of the centrum. The base of the lamelliform depressed transverse process (ib. *d*, *d*) is 1 inch 8 lines in extent, reaching within 2 lines of each articular end of the centrum. The longitudinal extent of the base of the neural spine is 1 inch. The characters of the corresponding vertebra in *Macropus rufus* are closely repeated, with the difference of size and slight increase of breadth over length, as in the sacrum; and these permit an inference that the tail in *Palorchestes* corresponded in strength, if not quite in relative length, to that in *Macropus*.

§ 4. *Palorchestes* (Os innominatum).—The pelvis of the Kangaroo is characterized by a long prismatic ilium, an oblong tuberosity above or anterior to the acetabulum, a "pectineal" or "ileo-pubic" process, the articular surfaces for the marsupial bones, the broad, compressed, subprismatic form of the ischium, the slenderness of the pubis, and the great length of both those elements of the pelvic arch.

The length of the pelvis due to the great extension of the os innominatum both in front and behind the acetabulum is a well-marked feature of resemblance to the same

* "Osteology of Marsupialia.—Part V.," Trans. Zool. Soc. vol. ix. p. 429, pl. lxxvi.

† Phil. Trans. 1874, p. 253.

part of the skeleton in the Bird, and similarly relates to the faculty of station and progression on the hind pair of limbs—the movement being, in the Kangaroo, as in some tribes of birds, by a series of hops, the fore limbs, however, in the mammal taking also an occasional share in progression on land, which is not permitted to the volant class.

The portion of pelvis (Plate 22) corresponding in size with the sacrum (Plate 21), although reduced to the parts immediately surrounding the acetabulum, includes the base of the ilium, showing its three-sided prismatic form, the precotylar tuberosity, and, above all, the "pectineal process" (ib. *e*), in size, shape, and position closely corresponding with that in *Macropus rufus* †.

The anterior or hæmal facet of the ilium (ib. fig. 1, ω) is more deeply excavated than in the recent Kangaroo; the rounded angle (*a*) dividing that facet from the inner or median facet (ib. fig. 2, ω′) is relatively thicker. The precotylar tuberosity (*d*) is more prominent, is relatively nearer the acetabulum; and a ridge is continued from the fore part of the tuberosity to the brim of that cavity, which more definitely or abruptly there defines the hæmal from the neural facets of the ilium than in recent Kangaroos.

The contour of the acetabulum is more ovate, the smaller end, at the fore part of the brim, being narrower in the larger fossil. The notch (*y*) at the hind part of the brim is narrower, and is nearly bridged over by the extension of the ischial (ω″) toward the pubic (ω‴) border of the notch; the depression (*x*) into which the notch expands at the bottom of the cup is relatively narrower in *Palorchestes* than in *Macropus*.

These characters would have indicated specific distinction if the present fossil had not exceeded in size the corresponding part in the largest living Kangaroos; the degree to which *Palorchestes* surpassed them is exemplified in the pelvis as in the skull.

Admeasurements of Pelvis.

	Palorchestes. in. lines.	*Macropus rufus.* in. lines.
Breadth of hæmal surface of ilium above the precotylar tuberosity	3 0	1 0
Breadth of neural surface of ilium above the precotylar tuberosity	3 3	1 3
Breadth of median surface of ilium below symphysial surface	2 0	1 0
Length of acetabulum	2 8	1 7
Breadth of acetabulum	2 6	1 4
Breadth of ischium behind the lower part of acetabulum	2 2	1 3

§ 5. *Palorchestes* (Femur).—The fossil thigh-bone, of which the two extremities are figured in Plate 23. figs. 1 & 2, shows an articular head (*a*) fitting the acetabulum of the pelvic fossil (§ 4). The height of the trochanter major (*f*), the length and backward position of the narrow trochanter minor (*n*), the depth of the cavity (*l*) under-

† Mem. cit. Trans. Zool. Soc. vol. ix. plates lxxix., lxxx., *c*.

mining the hind extension of the great trochanter, and the ridge (*p*) at the back part of the upper half of the shaft, bespeak the macropodal characters of the present fossil in the upper portion of the bone, as the partial division of the outer condyle (fig. 2, *v*) by the channel (*w*), and the deep rough oblong fossa (*y*) above that condyle, do in the lower portion *.

Guided by the proportions of the femur in *Macropus major* and *Macropus rufus*, I estimate the subject of fig. 1, Plate 23, to include the proximal third of that bone in *Palorchestes Azael*; and suspect, as the upper portion of the great trochanter is still epiphysial, or but partially united to the shaft, that this thigh-bone may have come from a not fully mature individual.

As in *Macropus rufus* the extreme breadth of the proximal end of the femur exceeds that of the distal end by 3 lines, I estimate the difference in those admeasurements of the ends of the fossil femur in Plate 23 to be within the limits of individual character in *Palorchestes*, the breadth of the shaft, where broken across, in both upper and lower portions being the same; and the circumference in both is 5 inches. The somewhat larger proportional proximal end, due to the development of the great trochanter, may be taken as one of the differential characters of the present huge femur as compared with that bone in the largest living Kangaroos.

The great trochanter is continued as a strong ridge (ib. fig. 1, *g*) $5\frac{1}{2}$ inches along the outer border of the bone; but the trochanter itself (*f*) is, relatively, less raised above the head (*a*) than in *Macropus major*. The articular surface of the head is less convex than in *Macropus rufus*, and the anterior concavity between it and the trochanter is less marked. The demarcation of the summit of the trochanter by the antero-internal channel is more feebly given in *Palorchestes*. The upper surface of the neck of the femur (*c*) is relatively broader in *Palorchestes* than in *Macropus*.

The lesser trochanterian ridge (*n*) is more posterior in position than in *Macropus rufus*, in which its free margin just comes into view when the femur is seen from the front †; this is not the case in *Palorchestes*, in which the ridge descends to the parallel of the beginning of the posterior ridge, which resembles at its most prominent part (*p*) a third trochanter ‡. The trochanterian fossa (fig. 1, *l*) has the extreme generic or family depth in *Palorchestes*; it forms a long narrow cavity, undermining the hinder basal part of the great trochanter.

From the summit of this trochanter (*f*) to the third trochanter (*p*) being $6\frac{1}{2}$ inches, the total length of the femur of *Palorchestes* may be reckoned, from the analogy of *Macropus rufus*, to have been not less than 18 inches; in that recent species it is $10\frac{1}{2}$ inches. The epiphysial line of the great trochanter is distinct, but confluence of the central part has kept the process in place in the present fossil.

The upper end of the linea aspera is preserved, expanding to form the process *p*.

* See the characters of the femur of *Macropus* described and figured in the Mem. cit. in Trans. Zool. Soc. vol. ix. p. 437, plate lxxxi.

† Mem. cit. *tom. cit.* plate lxxxi. fig. 1, *n*.

‡ See ibid. fig. 2, *p*, in *Osphranter rufus*.

At the distal end of the femur (ib. fig. 2) the chief distinction of *Palorchestes* from *Macropus* is in the relatively narrower postintercondylar fissure (*u*) and its minor expansion, where it is closed anteriorly*. The depression (*y*) is strongly marked in *Palorchestes*. The epiphysial line is traceable in the fossil; a wedge-shaped process at both the outer (*z*) and the inner (*z'*) borders rises as if to clamp more securely the epiphysis to the shaft.

The following admeasurements exemplify the difference of size between *Palorchestes Azael* and *Macropus rufus*, the measured femur of the latter being of a full-grown male:—

	Palorchestes Azael.	*Macropus rufus.*
	in. lines.	in. lines.
Extreme breadth of proximal end of femur . . .	4 9	2 9
Extreme breadth of middle of shaft of femur . .	1 8	1 0
Extreme breadth of distal end of femur	3 9	2 5

§ 6. *Palorchestes* (Tibia).—If the fine fragment of this bone figured in Plate 24 be compared with the corresponding views of the entire tibia of the large male Red Kangaroo figured in vol. ix. of the 'Zoological Transactions,' plate lxxxii., the association of the peculiar characteristics of the macropodal tibia with the grand proportions of that bone in *Palorchestes* will be readily appreciated.

The length of the present fossil remnant from the proximal end of the bone to the subsidence on the shaft of the procnemial plate is 7½ inches. The fore-and-aft diameter of the tibia, at the upper part of the plate, is 3 inches 5 lines; the span of the excavation between the procnemial and ectocnemial plates or ridges is 2 inches 4 lines; the antero-posterior diameter of the head of the tibia is 3 inches 10 lines; the breadth of the back part of the tibia, at 5 inches below the articular head, is 1 inch 6 lines. The head of the tibia is in a state of epiphysis; its undulatory course along the inner side of the bone is shown in fig. 4, but partial confluence, as in the case of the epiphysis of the femur of probably the same individual *Palorchestes*, has tended to retain the epiphysis in place, notwithstanding the movements and shocks of alluvial transport through which, seemingly, the fractures of the fossil are due.

The inner articular facet (ib. fig. 5), the only one preserved on the head, is relatively more extensive and more concave transversely than in *Macropus rufus*. The hind surface of the shaft, continued down from that articular surface, is thicker and more convex across; it contracts in the large recent Kangaroo to an angular ridge, sharply dividing the hinder from the antero-internal surface of the shaft of the bone.

The following are a few comparative dimensions of the tibia:—

* Compare fig. 2 with fig. 2, *u* (*Macropus rufus*) in plate lxxxi. of Mem. cit. Zool. Trans. vol. ix.

	Palorchestes Azael.		*Osphranter rufus.*	
	in.	lines.	in.	lines.
Length from head to subsidence of procnemial ridge	7	6	5	3
Fore-and-aft diameter at upper part of procnemial ridge	3	5	2	0
Transvere diameter of shaft halfway down procnemial ridge	1	7	1	0
Span of excavation between procnemial ridge and fibular ridge	2	4	1	6
Fore-and-aft diameter of head of tibia	3	10	2	8

§ 7. *Palorchestes* (Calcaneum).—In *Macropus* (*Osphranter*) *rufus* the length of the calcaneum exceeds the transverse breadth of the distal end of the femur by two sevenths; the extreme breadth of the calcaneum is one third greater than that of the middle of the shaft of the femur. By these proportions I am guided in the choice of the two fossil calcanea (figs. 4 & 5, Plate 23), and refer the longer bone to *Palorchestes*.

The length of the subject of fig. 5, Plate 23, exceeds the transverse breadth of the distal end of the femur (ib. fig. 2) by two sevenths. The length of the calcaneum (ib. fig. 4) exceeds the transverse breadth of the distal end of the femur (ib. fig. 3) by one fourth. The breadth of the calcaneal process of fig. 4 is equal to that of the longer calcaneum, fig. 5.

On the grounds subsequently to be adduced for concluding the leg and foot of *Procoptodon* to have been shorter in proportion to its length than in *Macropus*, I therefore assign the shorter and thicker calcaneum to that genus, together with the portion of femur (fig. 3), which shows more generalized characters, or those less strictly macropodal, than the femora assigned to *Palorchestes*, *Macropus*, and *Sthenurus*.

§ 8. *Macropus Titan* (Skull).—Of this species I am now enabled to add to maxillary and mandibulary evidences adduced in former Parts some instructive cranial characters.

The specimen yielding these was found by W. F. Tooth, jun., Esq., at King's Creek, near Clifton, Darling Downs, at a part of the bed which Dr. Bennett, F.L.S., had pointed out to his friend as being likely to yield fossils after a flood*. To these gentlemen the British Museum is indebted for the specimen. On receiving it as much of the adherent matrix was cleared away as could safely be meddled with; and the present state of the fossil is given in side and base views, of the natural size, in Plates 25 and 26.

It is a great part of the skull of a Kangaroo, wanting the lower jaw, but including the cranium proper, the interorbital and the hinder part of the facial division of the skull; also great part of the left zygomatic arch, with the included orbit and temporal fossa, the bony palate, and the molar dentition, of which the two hindmost teeth are sufficiently entire to afford the means of specific determination.

Other projecting parts and processes have suffered fracture, and the region of the

* See "A Trip to Queensland in search of Fossils," by Dr. George Bennett, F.L.S., in 'Annals and Magazine of Natural History,' April 1872.

large frontal sinuses has been obliquely crushed. The specimen is in the usual heavy petrified condition of fossils from the freshwater drift; it shows the effects of transport and attrition during the movements of this matrix before reaching the locality where it was found.

The first attention being directed to the teeth, of which the three last left molars and the four last right molars were in place, the characters of transverse lobes, links, and prebasal ridge were seen to be those of the genus *Macropus*, while the size and the sculpturing of the hind surface of the last molar (Plate 26. fig. 2) determined the species.

In *Macropus major* that surface (ib. fig. 3) is moderately hollowed lengthwise and thickly coated with cement, which partly fills the triangular transverse concavity, the apex of which shallows to the ordinary level of the hind surface before reaching the base of the crown. When the cement is removed the inner enamel boundary (fig. 3, *g*) is sharper and more produced than the outer one (ib. *h*).

In *Macropus Titan* the enamel, after coating the inner border of the hinder lobe, extends backward, downward, and outward, projecting as a sharp-edged ridge (ib. fig. 2, *g*), defining a deeper depression on the hinder surface of the tooth. There is also a shallow vertical groove (*h*) continued from the hind part of the apex of the inner border of the hind lobe downward toward the base of the crown, which groove seems to define the inner limit of the oblique posterior ridge. One sees that this groove repeats the deeper cleft that defines the mid link internally from the inner end or border of the anterior lobe. The oblique hind ridge (*g*) is indeed a serial repetition of the mid (*r*) and fore (*s*) links, but subsides with a more oblique course downward toward the base of the outer border of the hind lobe, having no other division of the molar to connect with such lobe. From the fore part of the base of the inner end of the hind lobe a low ridge defines the anterior surface of that lobe to the inner side between it and the mid link; this defining ridge is not present in the upper molars of *Macropus major*, but there is a small tubercle at the inner entry of the valley between the two main lobes of the upper molars in *Macropus major* which is not present in *Macropus Titan*.

The fossil skull, with the molars agreeing in the above characters and in size with those of more fragmentary examples of *Macropus Titan**, is of a mature and somewhat aged individual. The summits of both lobes of the hindmost grinder are worn so as to expose a linear tract of enamel, widest of course on the anterior lobe. In the penultimate grinder a broad field of dentine is exposed on this lobe, extending backward by a linear tract along the base of the mid link (*r*), but not so far as the transverse tract of dentine exposed on the hind lobe. In the antepenultimate grinder (m_1) both lobes are so worn that the lozenge-shaped fields of exposed dentine touch and communicate at the base of the worn-down link. The foremost grinder (d_4, Plate 26) is retained on the right side, worn down to its base; but this tooth has been shed on the left side, and

* Phil. Trans. 1874, plate xxi. figs. 8, 10, 15, 16; plate xxii. figs. 10, 12.

the grinding series reduced to the three true molars, as in old individuals of *Macropus major*.

The skull of this large existing species of Kangaroo which I have to compare with the present fossil retains the last deciduous molar (d^4) on both sides of the upper jaw, without any trace of the socket of the premolar which had worked in advance of the four retained grinders (d^1, m^1, ^{2}, ^{3}). In the maxillary fossil of *Macropus Titan* (figured in plate xxi. fig. 10, Phil. Trans. 1874) the two roots of p^3 are retained, the crown having been accidentally broken away. That of the last molar (m^3) had not come into place, although the front lobe had pushed its way out of the formative cell. The two lobes of m^2 in the same fossil show attrition of the enamel ridge, but not so as to reach the dentine.

In the younger subject of figs. 6, 7, 8 of the same plate and volume, the four teeth in place are d^2, d^4, m^1, and m^2; above the first of these is exposed the crown of p^3 in its formative cell, and part of that of m^3 is shown behind m^2.

The series of changes of the upper molar dentition of the extinct *Macropus Titan* are thus as instructively and almost as completely displayed in petrified specimens as in the existing species (*Macr. major*), of which I have obtained specimens in number and periods of age sufficient to exemplify these phases*. I have previously described a mandibular specimen of *Macropus Titan*, with the molar dentition reduced to m^2 and m^3†, as in the latest phase hitherto observed in *Macropus major*.

The cranial specimen exemplifying the reduction of molars to three on the left and four on the right side, lacks, unfortunately, the part of the upper jaw which supported the incisor teeth. Nearly two inches of the diastemal tract, however, is preserved in advance of d^4 on the right side. A fossil mandible of another individual of *Macropus Titan*, with a similar stage of dentition as the right side in Plate 26, fortunately gives the extent of the diastema between the molars and incisors‡; and guided by the proportion which this part bears to the upper diastema in *Macropus major*, I have restored in outline in Plates 25 and 26 what is wanting in the present fossil, together with an outline of the mandible and mandibular teeth.

The length of the mandibular diastema in *Macropus major* is 1 inch 9 lines, that of the maxillo-premaxillary one is 2 inches 6 lines. The length of the mandibular diastema in *Macropus Titan* being 2 inches 6 lines, that of the maxillo-premaxillary diastema, according to the pattern of the recent species, should be 3 inches 6 lines. There are indications, however, that the muzzle was relatively rather shorter in the larger extinct Kangaroo, and I have restored it with an interval of 3 inches 3 lines between the foremost molar and hindmost incisor.

Of this characteristic tooth fossil specimens reveal two patterns of the outer surface of the crown in examples indicative of species as large as *Macropus Titan* and *Sthenurus Atlas*.

In one type (Plate 25. fig. 4) the outer surface of the crown is divided into three

* See notes, p. 245, Phil. Trans. 1874. † *Tom. cit.* plate lxxvi. fig. 3. ‡ *Tom. cit.* plate xxvi. fig 11.

unequal convex tracts by two oblique grooves, of which the hinder one extends nearest to the base or root of the tooth; in the other type (ib. fig. 3) a deeper oblique fissure subequally bisects the crown; it marks off a more prominent fore part of the outer surface from a lower and vertically shorter, but rather more longitudinally extended, hind tract. As the first of these patterns is repeated in the third upper incisor of Kangaroos with a small premolar (*Macropus major**), and the second pattern is found in Kangaroos with a large trenchant premolar (*Halmaturus ualabatus*, *H. ruficollis*)†, I refer the fossils of the second pattern to *Sthenurus Atlas* and those of the first pattern to *Macropus Titan*.

The skull in this extinct species has the triangular form of occiput as in *Macropus major*, the apex of which, forming the summit of the superoccipital ridge, is somewhat rounded off. The upper and larger ends of the condyles subside more gradually into the occipital surface, and are not defined by a depression there as in *Macropus major*. The channel or concavity between the condyle and paroccipital is relatively wider in *Macropus Titan*. In this species the foramen magnum seems as if it had been notched at its upper border, where the exoccipitals may not have met, and where the foramen may have been bounded by an intercalated portion of the superoccipital.

As in *Macropus major*, also, a second inner ridge from the base of the paroccipital converges towards its fellow as it rises, parallel with the outer ridge, from the mastoid, but subsides before attaining the summit of the exterior ridge.

The crown of the superoccipital arch projects rather more backward in *Macr. Titan* than in *Macr. major*; it is not on a vertical plane with that of the occipital foramen, nor does it slope, as in many recent Kangaroos, forward from that foramen. The surface below the arch is traversed by a less prominent median vertical ridge in *Macropus Titan* than in *Macr. major*.

The upper border of the occipital foramen is mutilated in the fossil, but seems to have been more arched, less regular, than in *Macr. major*.

The basioccipital (Plate 26. fig. 1, ı) is carinate below, as in *Macr. major*‡; but there is more tumefaction at its suture with the basisphenoid in *Macr. Titan*.

A low crest runs along the line of the sagittal suture in the fossil, which bifurcates anteriorly, the divisions diverging to the postorbital prominences, which, as usual in the genus, are feeble. In *Macropus rufus*, at a similar phase of dentition with the fossil, the sigittal suture persists, and the low ridges bounding above the crotaphyte surfaces have not met at the mid line.

The fore part of the glenoid surface for the mandibular joint, in *Macropus Titan*, is contributed by the malar as in other Kangaroos. The outer surface of the zygoma seems not to have been so deeply impressed or concave as in *Macropus major* and *Macr. rufus*. The facial part of the skull anterior to the orbits is relatively broader in *Macr. Titan* than in either of the above-named existing species. The antorbital foramen is

* *Tom. cit.* plate xx. fig. 17.

† Ibid. figs. 20, 21.

‡ Also as in *Macropus rufus*: see "Osteol. of Marsupialia.—Part V.," Zool. Trans. vol. ix. pl. lxxiv. fig. 3.

relatively further from the orbit in *Macropus Titan* than in *Macr. major*; and in this character *Macr. rufus* more resembles the large fossil Kangaroo. The front pier of the zygoma springs from the side of the skull more posteriorly in *Macropus Titan* than in either of the large existing Kangaroos.

The bony palate (Plate 26) is extended further back, and the production of the alveolar border of the maxillary behind the last molar is more convex transversely than in *Macr. major* or *Macr. rufus*. The bony palate is entire in the fossil as in *Macr. major*, but is relatively wider than in that species; it has not the reticularly disposed small perforations shown by the specimen of *Macropus rufus* described in the 'Zoological Transactions'*. The interspace between the right and left ultimate molars in *Macr. Titan* is twice and two thirds of the fore-and-aft diameter of that tooth; in *Macr. major* that interspace equals two diameters and one fifth of the last molar.

The lower area or outlet of the zygomatic arch (Plate 26. fig. 1, *z*) is relatively larger in *Macr. Titan* than in *Macr. major*; it exceeds the length of the molar series of four teeth (d^4, m^1, m^2, m^3) by the length of m^3 in *Macr. Titan*, while in *Macr. major* the outlet does not equal in length the same series of teeth by one half of the anterior molar (d^4).

The diastemal border is less obtusely rounded in *Macr. Titan* than in *Macr. major*; it resembles more that border in *Macr. rufus*† and in some of the smaller existing Kangaroos (*Phascolagus erubescens*, e. g.). The extent of the diastemal interval in the upper jaw of the fractured fossil has been approximately estimated on the grounds above defined.

Subjoined are admeasurements of the fossil skull above described, and of that of a male at the same phase of dentition of a large existing Kangaroo.

	Macropus major.	*Macropus Titan.*
	in. lines.	in. lines.
Length of skull from superoccipital ridge to fore part of d^4	4 9	6 6
Breadth of skull at widest span of zygomata	4 3	5 9
Breadth of cranium at postorbital constriction	1 0	1 6
Breadth of cranium at the mastoids	2 11	3 8
Breadth of foramen magnum	0 10	0 11
Length of cranium from superoccipital ridge to post-orbital constriction	2 7	3 2
Length of cranium from superoccipital ridge to fore border of orbit	4 3	5 8
Length of orbito-temporal vacuity, lower opening	1 9	2 6
Breadth of orbito-temporal vacuity, lower opening	1 4	1 8
From hind border of palate to fore border of d^4	2 4	3 0
Breadth of palate between the right and left molars (m^2)	1 4	1 10
From alveolus of m^3 to hind border of palate	0 6	1 1

* Vol. ix. plate lxxiv. fig. 3.

† *Tom. cit.* plate lxxiv. fig. 3.

	Macropus major. in. lines.	*Macropus Titan.* in. lines.
From lower border of orbit to alveolar border at m_1	1 0	1 6
Length of series of four molars (d_4 to m_3)	1 10	2 2
Length of m_2 and m_3	1 1	1 3
Breadth of fore lobe of m_3	0 $4\frac{1}{2}$	0 6

§ 9. *Macropus Titan* (Femur).—An almost entire thigh-bone, in the same petrified condition as the skull above described, and from the same freshwater drift in King's Creek, offers the same proportions to that skull and to the mandible and teeth of *Macropus Titan* as the femur of *Macropus major* does to the same parts in that species. It is of the right side, in length 11 inches 6 lines; but would equal, if not exceed, a foot in length were the summit of the great trochanter entire. The bone is figured, of the natural size, in Plate 27, $2\frac{1}{2}$ inches of the middle of the shaft being omitted in figs. 1 and 2 to bring them into the quarto form. The macropodal characters of this fine fossil femur, and the deviations, besides size, from the femur of the largest existing Kangaroos, will be readily appreciated if Plate 27 be compared with plate lxxxi. Zool. Trans.* of the femur of *Macropus* (*Osphranter*) *rufus*.

A trace of the antero-internal groove, defining in that recent species the supertrochanterian tuberosity, is plain in the fossil at *e*, figs. 1 & 2, Plate 27, where that tuberosity has been broken away. Compared with the femur of *Macropus rufus* that of *Macropus Titan* shows a relatively wider and shallower concavity (ib. fig. 1, *d*) between the fore part of the great trochanter and the head (*a*) of the bone. The "cervix femoris" (*b*) is relatively thicker. The transverse diameter below the head is relatively greater, mainly through the greater extent of the bone internal to the "small trochanter" (ib. fig. 2, *n*), whereby that outstanding ridge-like process does not appear in a direct front view (ib. fig. 1). The same relative position of *n* in the femur of *Palorchestes Azael* is also due to the inward extension of the support of the neck and head of the bone.

The femoral shaft in *Macropus Titan* is relatively thicker, especially from before backward, than in *Macropus major* and *Macr. rufus*. The rough depression (ib. fig. 4, *y*) above the outer condyle is relatively larger, deeper, more sharply defined. The inner condyle (ib. figs. 1 & 2, *t*) has its inner (tibial) border better defined and produced so as to give a slight concavity, transversely, to that half of the back part of the condyle. This character is more marked in *Palorchestes* (Plate 23. fig. 2, *t*); but there is no trace of it in the inner femoral condyle of the large existing Kangaroos. The intercondylar notch (*u*, fig. 2, Plate 27) is narrower and deeper in *Macropus Titan* than in *Macropus rufus*, again repeating a femoral character of *Palorchestes*, but not in so marked a degree. The ectocondylar pit (ib. fig. 4, *v*) is equally well marked.

The broad shallow vertical groove at the back part of the outer condyle, which in *Macropodidæ* offers so interesting an approach to the characteristic structure of that

* Vol. ix.

part of the thigh-bone in Birds, is well shown in the femur of *Macropus Titan* (ib. fig. 2, *w*) as in that of *Palorchestes* (Plate 23. fig. 2, *w*).

The epiphyses are confluent with the shaft at both ends of the femur, but the line of separation is traceable in the fossil as in the figured femur of *Macropus rufus* above referred to.

I may here refer to portions of fossil femora which depart from the type of the two already described by deviating further from the characters of the femur in the existing species of *Macropus*. The chief difference is in the smaller and shallower depression (*y*) above the outer condyle, such depression being filled up, as it were, by a rough and thick ascending process of the distal epiphyses, of which a rudiment only exists in the femur of *Macropus Titan* (Plate 27. fig. 4, *z*) and of *Palorchestes Azael* (Plate 23. fig. 2, *z*). The femora with the larger and longer "clamping" process are thicker in proportion to their length than in the above-cited fossils, and still more so than in the recent Kangaroos. This stronger type is manifested by full-sized or mature femora of three dimensions, of which the distal end of the largest is figured in Plate 23. fig. 3. I shall at the conclusion of the present "Part" adduce evidence which leads me to deem these fossils to belong to the genus *Procoptodon*; and I, provisionally, refer the portion of femur figured and the shorter type of calcaneum in the same Plate (fig. 5) to *Procoptodon Goliah*.

§ 10. *Sthenurus Atlas* (Restoration of the teeth and part of the skull).—Confirmation of the ascription of the second type of upper third incisor to an extinct species of Kangaroo with a large premolar tooth has been had by the reception of a specimen of that part of the skull and dental system which, as a rule, is wanting in cranial fossils of these extinct Marsupialia.

This specimen consists of the facial part of the skull, from the anterior halves of the orbits to the ends of the premaxillaries, with their incisor teeth (Plate 25. fig. 2, Plate 26. fig. 4).

The molar dentition is represented by an anterior tooth of trenchant character (d_3), followed by three double-ridged molars on the left (Plate 25. d_4, m_1, m_2) and two on the right side (Plate 26. fig. 4, d_4, m_1). The third on the left (m_2) is emerging from its socket with the ridged summits of the lobes narrow; a portion of a formative cavity of a larger molar is preserved behind that tooth. This evidence of immaturity is supported by the incomplete exclusion of the crown of the third incisor (ib. ib. i_3); and the correspondence of the stage of dentition with the second (B) of the series in *Macropus major*, figured in my 'Anatomy of Vertebrates'*, was demonstrated by the usual test, viz. the exposure of the crown of the replacing tooth (Plate 26. fig. 4, p_3) in its formative alveolus above the deciduous teeth (d_3, d_4) in place and use. The third bilophodont tooth (m_2) on the left side is not so far advanced as its homologue in the jaw showing the third stage (*op. cit.* ib. c) of the dentition of *Macropus major*.

The germ of the premolar and the crowns of the deciduous teeth in place (d_3, d_4,

* 8vo, 1868, vol. iii. p. 380, fig. 296.

fig. 2, Plate 25, and fig. 4, Plate 26) accord with the characters shown in more fragmentary specimens of *Sthenurus Atlas*. Consequently can be added by means of the present fossil the characters of the first and third upper incisors to the previous knowledge of the dentition of that large extinct species.

The fossil evidence of this young individual of *Sthenurus Atlas* presents a condition which significantly points to the nature of its violent death, and to the operation of the powerful jaws and teeth of its carnivorous destroyer.

The upper jaw, anterior to the orbits, has been nipped in by a cross bite; another grip in a vertical or obliquely vertical direction in the orbital region has crushed the right half in the course of the interfrontal and internasal sutures to a lower level than the left half, with a similar degree of forward dislocation. The skull has been subject to this violence in its fresh state, and the matrix has subsequently become petrified about it, and has preserved the dislocations.

If they had been due to movements of the matrix after fossilization, the petrified head would show fracture corresponding to the bone; but no such evidence of posthumous crushing of matrix and fossil being present, I presume that the skull, if it had been imbedded uninjured, would have retained its form when petrified, and conclude that the actual state of the fossil was that in which it was interred before petrifaction began.

The anterior incisor (Plate 25. fig. 2, $i\,1$) is curved, as in most existing Kangaroos; but besides its superiority of size to that in the largest kind, as shown by the breadth of the crown*, the exserted and enamelled portion is both absolutely and relatively longer, and thus makes a nearer approach to the character of the first upper incisor in *Diprotodon*†. The convex or fore surface of the crown of $i\,1$ in *Sthenurus Atlas* is traversed longitudinally by a shallow and rather wide groove behind the mid line of that surface, which groove deepens near the cutting-edge, and thus marks it with a feeble notch. The enamel also shows some fine longitudinal striations. This wrap of the tooth is uninterrupted, but becomes much thinner at the back part. A transverse section of the crown would give a long, narrow oval, rather broader at the outer and hinder end.

The breadth of the tooth, or length of the oval, is 10 millims., or $4\frac{3}{4}$ lines; the thickness or antero-posterior extent is 4 millims., or $2\frac{1}{2}$ lines. The hind margin of the tooth, near the cutting-edge, shows the shallow indent caused by the crown of the second incisor; but this tooth in both premaxillaries has been displaced by the lateral crushing of these bones in the recent state, and was probably lost prior to the imbedding of the skull. The second incisor is the smallest and least deeply implanted in most Kangaroos.

The third incisor (Plate 25. fig. 2, $i\,3$) had not been fully developed; its crown had only partially emerged from the socket, whence its preservation. It is in the form of a

* Compare with Phil. Trans. 1874, plate xx. fig. 17 (*Macropus major*).

† Phil. Trans. 1870, plate xxxv. fig. 1, $i\,1$.

scalene triangle; the shortest side is turned forward, the longest side forms the cutting-edge, which is notched anteriorly by an oblique groove extending from near the middle of the outside of the crown down to the cutting-edge, then inward and forward along that edge to near the antero-inferior angle of the crown. The grooved part of the edge in its present narrow condition thus presents two trenchant borders. The fore side or border of the crown shows an anterior low convex ridge through the subsidence of the enamel between this and the mid groove; the enamel behind this groove is again at a lower level, thus the antero-posterior lay of the outer enamel is undulated. The fore-and-aft extent of the exposed crown is 6 lines, the front border or side of the triangle measures 5 lines.

The indent caused by the missing second incisor is present on both right and left anterior incisors; the interspace between the first and third incisors, from which the second has been pushed, is greater in the left than in the right premaxillary.

A detached fully developed third incisor of a full-grown *Sthenurus Atlas* is figured in Plate 25. fig. 3.

In the lower jaw of this species* the interval between the molars and procumbent incisor is less than in *Macropus Titan*†. The present specimen shows that a similar character marks the upper jaw. The extent of the maxillo-premaxillary diastema is here 10 lines, but would be of course greater in the full-grown Kangaroo.

The anterior molar (Plate 25. fig. 2, Plate 26. fig. 4, d_3), with a crown 6 lines in antero-posterior extent, shows a depressed middle tract of the outer surface traversed by two vertical ridges. The inner surface, which forms posteriorly a prominent convex lobe, sinks rapidly to a basal ridge as it extends forward to a low angle on the inner side of the anterior division of the tooth. The second molar (d_4) has a prebasal ridge without the fore link; the mid link is small and low placed, in chief continuation with the inner angle of the fore lobe. The hind surface of the hind lobe has a triangular excavation.

These characters are repeated in m_1 and m_2; the crown of the latter is protruding from the formative cell, and is unworn. The crown of the premolar, exposed in its formative cavity (Plate 26. fig. 4, p_3), is incomplete with the concomitant wide and deep excavation at the basal part for the unexhausted pulp. The longitudinal grooves and ridges of the trenchant apical border, part of which are visible in the worn premolar of the subject of a former Part‡, are well shown in the germ of the premolar in the fossil now described. The fore-and-aft extent of the crown agrees with that of the fully developed homologue, viz. 9 lines=18 millims.

The bony palate, so far as it is preserved, appears to have been entire.

§ 11. *Sthenurus Brehus* (Restoration of dentition and part of the skull).—This species was founded on a maxillary portion of cranium with the left molar series, in part mutilated, and with the last two molars of the right side (Phil. Trans. 1874, plate xxvii. figs. 5 & 6); also on a fragment of the left maxillary with the premolar and contiguous

* Phil. Trans. 1874, plate xxii. fig. 5. † Ib. ib. fig. 13. ‡ Ib. plate xxiv. fig. 4, p_3.

molar entire (ib. figs. 7, 8, & 9) from a younger individual. Both fossils were from MITCHELL'S Breccia-cave in Wellington Valley, New South Wales, and formed the first evidence of this extinct species which came to my hands.

Since the publication of the paper (*loc. cit.*) illustrative of these fossils I have been favoured, through the persevering and successful quest of GEORGE F. BENNETT, Esq., with portions of the skull and lower jaw of older and younger individuals of the same species from the freshwater drift at Clifton, Queensland. One of these specimens exhibits the entire molar series, left side upper jaw, with that of the right side, less the last molar; another fossil includes the premaxillaries and upper incisors; and a third consists of the fore part of the mandible with the lower incisor and with the first three molars of the right side. All three specimens are parts of the same skull.

A fourth lot consisted of four portions of the upper jaw of a mature but younger individual than the subject of plate xxvii. *loc. cit.*, and included the incisors and premolars of both sides, and the entire molar series of the right side.

A fifth specimen consisted of the fore part of the upper jaw of an aged individual with much of the crowns of the incisors worn away, and the smaller ridges on the inner side of the premolars rubbed smoothly down.

These specimens instructively exemplify the constancy of the maxillary molar characters of the genus and species as shown in the type specimen, and add those of the mandible and the characters of both upper and lower incisors.

Of the upper incisors the first or foremost (Plate 28. figs. 1, 2, & 3, i_1) has a greater relative superiority of size over the second and third than in any existing species of Kangaroo that has come under my observation; in this character *Sthenurus* approaches the Koalas and Potoroos among existing, and the colossal Diprotodonts among extinct Marsupials.

The transverse diameter of the crown of i_1 is 8 lines (17 millims.); it nearly equals that of the two following incisors, of which the third (i_3) is broadest, viz. 5 lines (10 millims.) along the oblique trenchant or working border; the thicker, triturant surface of the second incisor is 4 lines (8 millims.) in longest diameter. The crowns of the six incisors describe a semicircle (ib. fig. 3); those of the anterior pair, separated by a line's breadth in the fossil, evidently touched each other in the living animal at their median angles, which show the effects of mutual pressure.

Each incisor is curved lengthwise, with a strong outward or forward convexity; the exposed enamelled crown of the first measures in a straight line 1 inch 1 line (27 millims.), that of the second incisor 7½ lines (15 millims.), that of the third incisor the same; this, as usual, expands to the working surface; its outer enamel is bisected by a feeble linear longitudinal groove. The transverse interval between the two incisors of the third pair is 1½ inch.

The outer half of the fore surface of the crown of the second incisor (i_2) is prominent, and is pressed into a corresponding channel of the hind surface of the first incisor; the channelled part of the contiguous surface of the second incisor reciprocally receives

the prominent part of the opposed first incisor; the crown of the third incisor (i_3) presses closely against that of the second: thus firmly interlocked the three incisors in each premaxillary worked as one tooth. The enamel of the second and third incisors is continued from the outer or fore part of the crown upon part of the hind or inner surface; but the enamel of the large anterior incisor is limited to the fore part. In both proportion and curvature the large incisor resembles the homologous tooth in *Nototherium* and *Diprotodon*; but it is an incisor of limited growth, and its implanted fang tapers to the end, as in the rest of the family *Macropodidæ*.

From the back of the median border of the front incisor (Plate 28. fig. 3, i_1) to the fore border of the "foramen incisivum" (ib. *a*) is 1 inch 6 lines; from this border a groove is continued forward, shallowing, to near the tooth.

The breadth across the outsides of the last pair of incisors is 1 inch 11 lines; the breadth of the palatal part of the premaxillaries at the fore part of the prepalatal or incisive foramina is 1 inch 10 lines. From the third incisor to the premolar is 2 inches 1 line; in other words, this is the extent of the diastema or toothless space (Plate 28. fig. 1, *d*, i_3) between the incisors and the molars. The breadth of the bony palate anterior to the premolars is 2 inches 1 line.

To the objection that the species *Atlas* and *Brehus* of the genus *Sthenurus* might have been based, in Part VIII., on parts derived from the female and male of the same species, the reply is that, although the males exceed in size the females in most, if not all, Kangaroos, the difference is chiefly shown in the bones of the trunk and limbs, less so in the skull, and little, if at all, in the teeth.

Now the third incisor is, relatively to the first incisor, smaller in *Sthenurus Brehus* than in *Sthen. Atlas*. In the larger species the length of the molar series (Plate 28. fig. 1, p_3–m_3) is 3 inches 6 lines, in *Sthenurus Atlas* it is 2 inches 9 lines. The premolar (p_3) exceeds the rest in fore-and-aft diameter, which, as in the cave specimen (*loc. cit.* plate xxvii. fig. 7, p_3), is 9½ lines (20 millims.); the three low transverse ridges which connect the inner with the outer wall are well marked in the present comparatively young though full-grown individual. These ridges become less salient in the course of the oblique wear of the crown of the premolar from the outer to the inner ridge, and in old individuals they are polished off. But all the generic and specific characters of the premolar of *Sthenurus Brehus* from MITCHELL'S Breccia-cave in New South Wales are repeated in the present specimens from the fluviatile beds of Queensland. The same may be said of all the succeeding molars which in the type specimen are sufficiently complete for comparison. The last molar in the present example (Plate 28. fig. 3, m_3) has not quite come to the grinding level, and its ridges are untouched. The enamel-fold from the inner angle to the hind ridge, which defines by its oblique tract along the hind surface the angular depression there, seems as if it were folded on itself or notched at its basal termination.

The descending process of the zygoma is more perfectly preserved than in any other fossil hitherto transmitted to me of the genus *Sthenurus*; it terminates below the level

of the grinding-surface of m_2; in older examples it would show the same relation to m_3, as the grinders move, or seem to move, forward.

I next proceed to notice the portions of skull of a more aged individual of *Sthenurus Brehus* from Clifton, Queensland. The laterally crushed maxillary part of the skull includes, with the incisors, the entire molar series of the left side and the major part of that of the right side. The premolar with a fore-and-aft length of 10 lines (20 millims.) in the type specimen (*loc. cit.* plate xxvii. fig. 7, p_3) is but half a millimetre less in the present fluviatile fossil; and this seems due to the wear of the anterior prominence. But all the formal characters are closely repeated. I have had no evidence from the spelæan haunt of the Thylacoleons of a giant Kangaroo which had attained the experienced age of the original of the present Queensland fossil. The molar contiguous to p_3 contrasts, as usual, its great degree of wear with the fresher crown and higher level of the antecedent subsectorial tooth; the fore-and-aft diameter, 6 lines (12 millims.), is the same in both fossils; the minor transverse breadth in the Queensland specimen is due to the wearing down of the outer angles of the transverse lobes or ridges, which are prominent in the cave fossil. The superiority of size, slight as it is, in m_1 of the type subject of plate xxvii. figs. 5 & 6 (*loc. cit.*) is chiefly due to the minor wear of the crown of that tooth in the cave fossil. The last two molars occupy a longitudinal extent of 1 inch 6 lines (37 millims.) in both specimens. The linkless prebasal ridge is transverse, not curving at either end to be continuous with the corresponding angles of the fore lobe; the low, short mid link is less distinctly continued to the inner angle of the fore lobe than in *Sthenurus Atlas*; the depression on the hind surface, due chiefly to the ridge curving from the inner and hinder angle of the hind lobe toward the outer side of the base of the crown, with the lower and shorter ridge from the outer angle, are all characters of *Sthenurus Brehus*, repeated in the present as in the preceding Queensland sedimentary fossil.

The left molar series in this instructive specimen occupies a longitudinal extent of 3 inches 3 lines.

The dentine is exposed on the fore lobe of the last molar, and the fore part of the enamel ridge of the hind lobe is nearly worn through; the prebasal ridge also shows abrasion. A hollow transverse field of dentine is exposed on both lobes of the penultimate molar. With these indications of greater age the maxillary pier has retrograded and projects on the transverse parallel chiefly of the last, instead of the penultimate, molar as in the younger specimens (plate xxii. *loc. cit.*). In all the bony palate is entire.

The fore part of the present skull shows a diastema 2 inches in extent. From the back of the socket of the third incisor to the fore part of the crown of the first is 1 inch 3 lines. Of the third incisor, the seat of variety in existing Kangaroos, the left is lost, and of the right one only the fang remains. The crown of the second right incisor is worn nearly to its base. The first or front incisor is present in both premaxillaries, with its fang exposed in the left one. The crown is worn to the level of the palate;

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the smooth and polished surface (Plate 28. fig. 5) presents an oval figure, the great end outward; the long diameter is 7½ lines (15 millims.), the short diameter, near the outer side of the worn surface, is 5½ lines (11 millims.). The enamel, nearly 2 millims. in thickness, is limited to the anterior surface, bending slightly back at the outer and inner margins; not more than 9 lines in length of the enamelled crown remains. The whole incisor, as usual, is curved lengthwise, with the greater convexity anterior; the root contracts to its implanted end; the length of the incisor, in a straight line, as here worn, is 1 inch 8 lines. The portion of cranium preserved, from the fore part of the front incisor to the back of the last molar, measures 6 inches 8 lines. About 2 inches of the facial part of the premaxillaries are preserved, bounding by a curved and obtuse border, thinning as it rises, the anterior nostril (Plate 28. fig. 1, *n*). According to the proportions of some existing Wallabies, which retain the premolar with the last molar in use, 5 inches may be added for the extent of skull behind the last molar, and the total length of the skull in *Sthenurus Brehus* may be moderately estimated at 12 inches.

The skull, so far as it is shown in the present specimen, has been crushed sideways, not partially as in the cave fossil, but by a pressure operating along a more extensive plane, and which I deem to be due to movement of the matrix, rather than to the jaws of a destroyer or devourer.

The lower jaw, which appears to have been imbedded originally in connexion with the upper one, has suffered similar lateral compression. Only the fore part of the mandible has been obtained or transmitted: it includes the pair of lower incisors with the premolar and two following molars of the right side; these are much worn. The length of the diastema is 2 inches: in *Sthenurus Atlas*† it is 1 inch 3 lines. In the course of the pressure to which this mandible of *Sthenurus Brehus* has been subject, the attachment of the broad symphysis has been overcome, and the right ramus has been moved a little in advance of the left.

The thin alveolar sheath does not extend to, or has been lost from, the end of the cement-clad root next the enamelled crown. This expands as it extends forward, and terminates in a polished worn surface, 10 lines in long diameter (obliquely transverse), 5 lines in fore-and-aft diameter. The length of the enamelled (under or outer) part of the crown is 8 lines, that of the entire tooth is 2½ inches. The fang, as usual, tapers as it recedes in its socket (Plate 28. fig. 1, *i**). The narrow symphysial border sinks from the premolar alveolus with a sharp curve before extending forward to expand upon the terminal part of the socket of the incisor. The outlet of the dental canal (*v*) is nearer the molars, and the diastema, with the symphysial part of the ramus, is longer, relatively, than in *Sthenurus Atlas*.

A third example of the premaxillary part of the skull with the fore part of the right maxillary, of a still older individual of *Sthenurus Brehus* from Queensland deposits, shows the six incisors *in situ*, much worn, and the form and transverse extent of the palate between those teeth and the molars. The length of the diastema is 2 inches

† Phil. Trans. 1874, plate xxii. fig. 5.

1 line, the breadth of the palate at the prepalatal foramina is 1 inch 9 lines. These foramina are elongate, from 2 to 3 lines broad, about 6 lines long, and continued forward by a groove (ib. *b*), which shallows out when parallel with the third incisors. These are much worn; the working-surface of the third is 7 millims. by 6 millims. The enamel, which is continued from the outer upon the hinder surface, is impressed, as in the less-worn tooth of the younger *Brehus*, by a longitudinal groove almost equally bisecting the outer surface. The second or mid incisor is worn almost to the stump. The first pair of incisors, being more worn than in the subject of figure 4, show a working surface of similar shape but rather smaller dimensions; the anterior coat of enamel is reduced to a length of 4 lines (10 millims.).

In the collection of Marsupial fossils from Queensland in the Museum of the Natural-History Society at Worcester, I noted, in 1858, the left lower incisor of a Kangaroo, of which I made drawings of the under or outer side (Plate 28. fig. 4). This tooth best agrees with the corresponding incisor of *Sthenurus Brehus*. It had preserved an extent of enamelled crown of 8 lines, the breadth being that of the more worn incisor of Plate 28. fig. 5. In the large existing Kangaroo (*Macropus major**) the breadth of the crown of the lower incisor is $4\frac{1}{2}$ lines, in *Macropus* (*Osphranter*) *rufus* it is barely 4 lines.

The portion of skull of a *Sthenurus Atlas* (Plate 25. fig. 2, Plate 26. fig. 4) permits comparison to be made of the first and third incisors with those teeth in *Sthenurus Brehus*. The first incisor is but half the size of that in the larger species, while the third incisor presents a crown of equal size. The generic character of equal division of the crown by the longitudinal groove is retained, but the anterior border of the groove is produced at the lower part of the crown. Such character, however, may have existed in the part of the crown worn away in the subject of Plate 28. fig. 1, *i* 3. But the difference of proportion in the upper incisors is, at least, specific. In *Macropus Titan* (Plate 25. fig. 4) the modification of the pattern of the third incisor is associated with generic distinction in other parts of the dental system and in the skull itself.

§ 12. *Macropus affinis* (Metatarsus).—The hind foot in *Macropodidæ* exhibits an extreme modification of its bony structure. The inner toe (I) is suppressed; the metatarsals of II & III are long and filamentary, supporting a pair of small pendent fur-cleansing claw-toes; that of IV is both long and large, with characteristic modifications of its proximal end; that of V is much less, the shaft compressed, but supporting, like that of IV, a toe with a *quasi* hoof for station and progression.

In Plate 29. fig. 4 is given a view of the fourth and fifth metatarsals, natural size, of the right hind foot of the large male *Macropus* (*Osphranter*) *rufus*, already referred to. Two other views of the same bone will be found in the paper "On the Osteology of the Marsupialia" in the Zoological Transactions†.

In the task of determining the fossil specimens of the homologous bones, those best agreeing in proportions with the corresponding metatarsals of existing Kangaroos were set apart from the fossils deviating in a marked degree from such proportions.

* Phil. Trans. 1874, plate xx. fig. 15.

† Vol. ix. plate lxxxiii.

In the first group was the upper two thirds of a left fourth metatarsal (Plate 30. figs. 7, 8, & 9) with a proximal articular surface of the same breadth as in *Macropus rufus* and *Macropus major*, but with a markedly thicker shaft, being broader from side to side in proportion to the depth from before backward. The smooth tendinal groove answering to that marked *n* in figure 4, Plate 29, on the fore part of the shaft in *Macropus rufus*, was bounded in the fossil (which I have noted, for convenience, as from a *Macropus affinis*) by stronger ridge-like risings, and the groove does not reach so far down the fibular half of the anterior surface of the bone. On the tibial side of the tibial ridge of this groove the fore part of the shaft shows a slight concavity in *Macropus affinis*, whereas in both cited species of the large existing Kangaroos the answering part of the metatarsal is transversely convex. At the back part of the proximal third of the shaft the rough surface or ridge for muscular attachment is more prominent, better defined, yet less extended longitudinally, in the fossil. This specimen is from King's Creek, Darling Downs, Queensland.

§ 13. *Phascolagus altus* (Metatarsus).—A right fourth metatarsal (Plate 30. figs. 1–5) from the same formation and locality has come from a larger kind of Kangaroo than *Macropus affinis*. It is an inch longer than the subject of figure 4, Plate 29 (*Macropus rufus*), is relatively thicker, and, like the previous fossil, differs in presenting a stronger ridge bounding the fibular side of the anterior surface of the shaft. This part of the bone is also more prominent, giving a convexity to the outline of a side view (ib. fig. 3) not present in the fourth metatarsal of *Macropus major* or *Macr. rufus**. The present fossil likewise shows a relatively broader distal end (ib. fig. 6), which is barely 1 line less in transverse diameter than is the proximal end (ib. fig. 5). On this surface, as in *Macr. rufus* and *Macr. affinis*, the hinder prominence shows the oblique tendinal groove (ib. fig. 4, *g*) and the flat inferior facet (*h*) for the articulation of the large tarsal sesamoid†. The fibular or outer side of the proximal end, in both fossils, shows, as in the recent Kangaroos, the antero-posteriorly prolonged, bilobed, articular surface (ib. fig. 2, *m*, *n*) for the side of the head of the fifth metatarsal. Below this surface is the depressed rough tract (ib. *k*), continued down nearly three fourths of the back third of the fibular side of the shaft, for the ligamentous attachment of the smaller compressed shaft of the fifth metatarsal. The posterior ridge in the present metatarsal, which I refer to a *Phascolagus altus*, answering to that marked *d'* in Plate 29. fig. 6 (*Macropus affinis*), is continued lower down, nearly to the end of the shaft. The hinder half of the distal articular surface (Plate 30. fig. 6) is fashioned by a mid rising into a double trochlea, as in existing Kangaroos.

§ 14. *Palorchestes* (Metatarsus).—The breadth of the middle of the shaft of the fourth metatarsal of *Macropus rufus* is two thirds that of the same part of the femur. The breadth of both fourth and fifth metatarsals, naturally united one third down, is nearly equal to three fourths of the breadth of that part of the femur.

The breadth of the middle of the shaft of the fourth metatarsal, the subject of

* See figs. 1 & 2 of plate lxxxiii. Zool. Trans. *tom. cit.*

† See Cut, fig. 2, p. 441, Zool. Trans. *tom. cit.*

Plate 29. fig. 1, is two thirds that of the same part of the femur, as shown at the broken ends in figs. 1 & 2 of Plate 23. The breadth of the naturally united fourth and fifth metatarsals (Plate 29. figs. 1 & 2), one third from their proximal ends, equals four fifths of the same part of the femur of *Palorchestes Azael*.

To this species, therefore, I provisionally refer the fossil subjects of figs. 1, 2, and 3 of Plate 29. The length of the fourth metatarsal in those figures is restored in outline from an entire homologous bone of the same extinct species which had become detached from the contiguous metatarsals, and which I have not thought necessary to figure.

In the fossil under description, to the great fourth metatarsal lacking the distal end there remained attached the fifth metatarsal (ib. figs. 1 & 2, v), wanting only a portion of the plantar or posterior wall of the proximal end; and, similarly attached, the proximal half of the third metatarsal (ib. ib. iii), exhibiting the characteristic macropodal slenderness. It is interesting to note, however, that the fifth metatarsal in the huge extinct Kangaroo shows more nearly the normal proportions of the bone than in the existing species, even the largest, as, e. g., *Macropus rufus* (Plate 29. fig. 4, v); and the more slender third metatarsal bone of *Palorchestes* (iii, fig. 2, Plate 29) is relatively less atrophied than in existing Kangaroos. Its proximal end (ib. fig. 3, iii) presents an oblong, subquadrate, almost flat surface for the ectocuneiform, and a triangular surface on the inner side (ib. fig. 2, *b*) of the proximal end for part of the head of the second metatarsal, which bone is wanting in the fossil. It articulates with the tibial side of the proximal end of the fourth metatarsal by a surface which is extended by the backwardly directed process (ib. fig. 2, *c*). Below the articular head (ib. *a*–*c*) the shaft narrows and becomes compressed in its upper third, below which it assumes a subtrihedral figure, with a trenchant margin both before and behind along its upper fourth.

The shaft does not exceed 2 lines in breadth at the point of fracture (*d*). The bone closely adheres, either by anchylosis or matrix, to the shaft of the great fourth metatarsal, inclining from the inner (tibial) side to the plantar aspect of the shaft, as does the corresponding metatarsal in *Macropus rufus**. The proximal articular surface of the fourth metatarsal (Plate 29. fig. 3, iv) presents an undulating tract adapted to the distal surface of the cuboid; its broadest rotular (anterior) half is gently convex transversely at the fibular half, concave at the tibial half; the narrower plantar or posterior subquadrate tract is feebly concave rotulo-plantad, almost level transversely; this tract extends plantad, or backward, so as to overhang the shaft; it is grooved at *e*, fig. 3, by the "peroneus" tendon, which runs across the back or under (plantar) aspect of the tarsus to be inserted into the entocuneiform bone; also, as in existing Kangaroos and in *Macropus affinis*, it has a flat articular surface at the underside of the overhanging part for the large tarsal sesamoid. The inner or tibial side of the proximal end of the fourth metatarsal shows the two small vertical facets for the ectocuneiform, and a well-marked rough depression for the proximal ends of the third and second slender metatarsals.

* Zool. Trans. *tom. cit.* plate lxxxiii. fig. 1, iii.

The shaft of the great metatarsal of *Palorchestes* is subtrihedral; the rotular surface (ib. fig. 1, IV) is slightly concave transversely along its middle third as in *Macropus Titan*, not prominent as in *Macropus rufus* (ib. fib. 4). The plantar side (ib. fig. 2) is produced into a ridge, broad along the upper third (*o*), becoming sharper (*h*, *h*) as it descends, and subsiding about one half of the length of the bone (*o'*) from the distal end. The corresponding portion of the metatarsal of *Macropus rufus* (ib. fig. 6) is widely channelled where in the fossil it is angularly convex. The greatest rotulo-plantar thickness of the shaft in *Palorchestes* is 1 inch 4 lines, the greatest transverse thickness is 1 inch; that of the proximal end is 1 inch 6 lines, its rotulo-plantar thickness is 1 inch 5 lines.

The fifth metatarsal of *Palorchestes Azael* (Plate 29. figs. 1, 2, 3, V) is relatively much stronger than in *Macropus major* or *Macr. rufus* (ib. fig. 4, V). The plantar part of the proximal end, broken away in the fossil figured, is entire in a later acquired homologous bone of *Palorchestes*. This presents a small, oval, flat, vertical surface for the fourth metatarsal, a broader subtriangular one for the backwardly extended process of the cuboid*, and a larger horizontal facet for the surface, marked *l*†, of the same tarsal bone. The proximal articular surface of the fifth metatarsal is very small in proportion to the bone in *Palorchestes*. External (fibulad) to that surface the bone rises above the proximal end of the fourth metatarsal in the form of an antero-posteriorly extended thick round edge.

The shaft of the fifth metatarsal is subcompressed along the proximal three fourths; it measures 13 lines in rotulo-plantar thickness, one third down; and here, near the plantar side, its thickness (or tibio-fibular breadth) is 6 lines. The opposite (rotular) border is not sharp, as in *Macropus major* and *Macr. rufus*; but though thin, in comparison with the plantar surface, the border is rounded off. The shaft loses rotulo-plantar thickness and gains transverse breadth as it approaches the trochlear articular surface (V); this is 1 inch transversely, 10 lines where thickest from before backward. The surface is not simply convex, as in *Macropus rufus* (Plate 29. figs. 4 & 5, V), but is made trochlear by a plantar median ridge, on each side of which the surface, transversely, is feebly concave. The outer (fibular) side of the shaft has a feeble median longitudinal channel along the middle of the proximal two thirds. The upper half of the shaft shows in fractured portions of homologous fossils a small medullary cavity.

Thus we learn that in the large extinct Kangaroo of the genus *Palorchestes* the fourth and fifth digits were less unequal in strength, and the fifth took more share in station and locomotion than in the largest existing kinds. The metacarpal segment and the rest of the foot were proportionally broader; but the length of the fourth metatarsal in *Palorchestes* indicates, nevertheless, that it was a powerful leaper.

§ 15. *Procoptodon* (Metatarsal and Femoral Characters).—In deprecation of the foregoing details, more wearisome perhaps to the reader than the inditer, I may plead the

* "Osteology of Marsupialia," Zool. Trans. *tom. cit.* plate lxxxiii. fig. 11, *k*.

† Ibid. fig. 10.

great proportion of fragmentary evidences of the hind feet of large extinct Kangaroos as compared with entire or nearly entire bones. The grateful aid which such rare specimens have yielded has impressed me with the desirability, if not duty, of defining and recording all characters which may help future collectors, especially in Australia, in determining such fossil fragments which are likely to accumulate in the public and private museums of that great colony.

I refrain from trespassing on the time and means of the Society with the results of comparisons by which metatarsals of *Macropus Titan*, of the two dentally determined species of *Sthenurus*, and of some species of *Protemnodon* have been worked out. But, in regard to the extinct form of Kangaroo which has most interest in relation to its aberrant or transitional character, I cannot withhold evidences which give some clue to the characters of the hind limbs, and I finally pass to the result of the present researches which has yielded me perhaps most satisfaction.

I have alluded to the primary step in the survey of the vast series of metatarsal fossils which led to setting apart those indicative of a hind foot shorter in proportion to its breadth, and yet retaining unmistakable macropodal characters.

In the specimen, for example, of the naturally united fourth and fifth metacarpals figured in Plate 31. figs. 1–5, the fourth is thicker than, but is little more than two thirds the length of, the homologous bone in *Macropus rufus* (Plate 29. fig. 4). The fifth metatarsal (Plate 31. figs. 1, 2, 3, v) shows a greater degree of thickness, in proportion to its length, than in *Palorchestes Azael* (Plate 29. figs. 1 & 2, v).

The proximal end of the fourth metatarsal (Plate 31. fig. 4, iv), though somewhat mutilated, exhibits the characteristic modifications of the articular surface in the normal Kangaroos; and these characters are shown more plainly in the homologous bone of a larger kind of *Procoptodon* (ib. fig. 8, iv), viz. the non-articular peninsula (*f*), the backward or plantar production (*e*), with the terminal groove (*g*) for the tendon before mentioned; but this groove is less deep than in the type Kangaroos: the flat surface beneath (fig. 6, *h*) indicates a larger proportional sesamoid than in the species of *Macropus*.

The fore surface of the shaft of the fourth metatarsal (ib. fig. 2) is more even or flattened than in *Macropus affinis*, *Macr. Titan*, and the great recent kinds of Kangaroo. The distal end is more expanded, surpassing the proximal end in breadth. The ridge on the back part of the shaft (ib. fig. 1, *o*) is broader, less produced, and less extended downward than in *Macropus*, *Sthenurus*, or *Palorchestes*.

The well-preserved proximal end of the fifth metatarsal shows its apophysial production (ib. figs. 1 & 2, *z*) proximad of the articular surface of the fourth metatarsal. This process is absolutely as well as relatively longer than in *Palorchestes Azael*. As in that species three articular facets are present at this end of the bone, two for the cuboid and one for the contiguous (fourth) metatarsal, the cuboidal surfaces being relatively larger than in *Palorchestes*, and the tubercle projecting tibiad beyond the metatarsal surface is more developed in *Procoptodon*.

At the distal articular surface the chief difference is seen in the greater production of the tibial convexity of the trochlea. By reason of this prominence its preservation is rare in the rolled fossils of the present form of metatarsal from the creek-beds of Queensland.

Of the metatarsals of this shorter type three modifications are shown by the fossils that have reached me, which are indicative of three species of *Procoptodon*. The metatarsal (Plate 31. figs. 10–12), of equal length with that (ib. figs. 1, 2) of *Procoptodon Pusio*, but more slender, I take to be from a female Kangaroo of that species.

Deeming it probable that the form (family or genus) of Macropodal Marsupials which, by dental and mandibular characters, offered the nearest approach to the large isopodal or gradatorial family (*Diprotodontidæ*) would present a corresponding approach thereto in the form and proportions of the hind foot, I refer the present type of metatarsal bones to the genus *Procoptodon*.

In this genus the above-described representative of the smallest known species would answer, as to size, to the evidences which have been given of the maxillary, mandibular, and dental characters of *Procoptodon Pusio**.

The specimens next in size (Plate 31. figs. 6–9) I refer, on similar grounds, to *Procoptodon Rapha*†.

Parts of a hind foot of a still larger species similarly relate to *Procoptodon Goliah*‡. Save in size, the characters of the metatarsal about to be described so essentially resemble those of the homologous bone in Plate 31, that I have not thought it reasonable to devote to it an additional Plate.

This metatarsal, the fourth, is 5 inches 3 lines in length, with a proximal breadth of 1 inch $5\frac{1}{2}$ lines, the opposite dimension being 1 inch 3 lines. The fore part of the cuboidal surface is relatively broader from before backward than in *Procoptodon Pusio*. There is no indication of the proximo-tibial ridge (*x*, fig. 10, Plate 30), in which character the present bone resembles its homologue in *Procoptodon Rapha*.

The posterior angle at the proximal half of the shaft is less marked and less produced than in *Procoptodon Pusio*. The posterior depressions above the distal trochlea are deeper and better defined than in *Procoptodon Rapha* or *Procop. Pusio*.

The fifth metatarsal of *Procoptodon Goliah* is 5 inches in length; the greatest diameter of the shaft is 1 inch, equalling that of the homologous bone in *Palorchestes Azael*, which is more than one fourth longer. The tibial covexity of the distal trochlea is less produced than in *Procoptodon Rapha*, and the whole hind surface of the joint is less obliquely disposed than in that species or in *Procoptodon Pusio*.

Thus the resolution of these shorter and stouter metatarsals into three categories, characterized by modifications of shape as well as by size, concurs with the previously adduced evidences of jaws and teeth in showing that the procoptodont modification of *Macropodidæ* was of old manifested by Australian Kangaroos under three specific forms.

* Phil. Trans. 1874, p. 788, plate lxxvii. figs. 2–7.

† Ib. p. 788, plate lxxvii. figs. 8–12, plate lxxviii.

‡ Ib. p. 791, plates lxxix., lxxx.

But these, which my present materials have enabled me to define, may prove not to have been the only links connecting the saltigrade with the gravigrade groups of phytiphagous Marsupials.

Description of the Plates.

PLATE 19.

Fig. 1. Portion of right mandibular ramus and teeth of *Palorchestes Azael*, Ow.
Fig. 2. Working-surface of the same teeth.
Fig. 3. Hind fractured surface of the same fossil.
Fig. 4. Inner side view of last lower molar of *Palorchestes Azael*.
Fig. 5. Upper view of part of left mandibular ramus with teeth and stumps of the same species.
Fig. 6. Outside view of the molar (m_1) of left mandibular ramus of the same.
Fig. 7. Inside view of the same molar.
Fig. 8. Back view of the same molar.

PLATE 20.

Left side view of the fore part of the skull and teeth of *Palorchestes Azael*: the entire skull and dentition restored in outline.

PLATE 21.

Fig. 1. Hæmal (under or front) view of the sacrum and first caudal vertebra of *Palorchestes Azael*.
Fig. 2. Right side view of first caudal vertebra of the same.
Fig. 3. Neural (upper or back) view of the same.

PLATE 22.

Fig. 1. Outer side view of part of right "os innominatum" of *Palorchestes Azael*.
Fig. 2. Inner side view of the same.
Fig. 3. Transverse section of ischium at ω, fig. 1.
Fig. 4. Transverse section of pubis at ω_1, fig. 2.
Fig. 5. Acetabulum of *Procoptodon Goliah* (?).

PLATE 23.

Fig. 1. Back view of proximal portion of right femur of *Palorchestes Azael*.
Fig. 2. Back view of distal portion of the left femur of the same.
Fig. 3. Back view of distal portion of right femur of *Procoptodon Goliah*.
Fig. 4. Upper view of right calcaneum of the same.
Fig. 5. Upper view of left calcaneum of *Palorchestes Azael*.

PLATE 24.

Fig. 1. Fibular (outer) side view of proximal portion of left tibia of *Palorchestes Azael*.
Fig. 2. Rotular (front) view of the same.
Fig. 3. Popliteal (back) view of the same.
Fig. 4. Tibial (inner) side view of proximal end with epiphysis of the same.
Fig. 5. Tibial (inner) proximal articular surface of the same.

PLATE 25.

Fig. 1. Left side view of cranium, with skull restored in outline, of *Macropus Titan*.
Fig. 2. Left side view of fore part of cranium of a young *Sthenurus Atlas*.
Fig. 3. Outside view of left upper third incisor of *Sthenurus Atlas*.
Fig. 4. Outside view of crown of left upper third incisor of *Macropus Titan*.

PLATE 26.

Fig. 1. Under or base view of cranium, with skull restored in outline, of *Macropus Titan*.
Fig. 2. Hind surface of last molar (m_3) of the same.
Fig. 3. Hind surface of last molar of *Macropus major*.
Fig. 4. Under view of fore part of right upper jaw and teeth of a young *Sthenurus Atlas*.

PLATE 27.

Fig. 1. Front view of right femur (omitting 2 inches of shaft) of *Macropus Titan*.
Fig. 2. Back view of right femur (omitting 2 inches of shaft) of the same.
Fig. 3. Inner view of proximal end of right femur of the same.
Fig. 4. Outer view of distal end of right femur of the same.

PLATE 28.

Fig. 1. Outside view of parts of right upper and lower jaws and teeth, with part of the skull restored in outline, of *Sthenurus Brehus*.
Fig. 2. Upper view of premaxillaries and incisors of the same.
Fig. 3. Under view of the same fossil.
Fig. 4. Under view of right mandibular incisor of *Sthenurus Brehus*.
Fig. 5. Upper surface of worn end of right mandibular incisor of an aged *Sthenurus Brehus*.

PLATE 29.

Fig. 1. Front view of metatarsals IV and V and part of III of *Palorchestes Azael*.
Fig. 2. Back view of the same.
Fig. 3. Proximal (upper) articular end of the same.
Fig. 4. Front view of metatarsals IV and V, with part of cuboid, of *Macropus rufus*.
Fig. 5. Back view of distal portion of the same.
Fig. 6. Back view of upper two thirds of fourth metatarsal of *Macropus affinis*, Ow.

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PLATE 30.

Phascolagus altus.

Fig. 1. Front view of the right fourth metatarsal.
Fig. 2. Outer side view of the same.
Fig. 3. Inner side view of the same.
Fig. 4. Back view of the same.
Fig. 5. Proximal articular surface of the same.
Fig. 6. Distal articular surface of the same.

Macropus affinis.

Fig. 7. Outer side view of portion of the right fourth metatarsal.
Fig. 8. Back view of part of the same.
Fig. 9. Proximal articular surface of the same.

Undetermined Species.

Fig. 10. Front view of proximal phalanx of fourth toe of an extinct Kangaroo, of the size of *Phascolagus altus*.

PLATE 31.

Fig. 1. Back view of metatarsals IV and V of *Procoptodon Pusio*, Ow.
Fig. 2. Front view of the same.
Fig. 3. Outer side view of the same.
Fig. 4. Proximal (upper) articular end of the same.
Fig. 5. Distal (lower) articular end of metatarsal IV of the same fossil.
Fig. 6. Back view of metatarsals IV and V of *Procoptodon Rapha*, Ow.
Fig. 7. Outer side view of metatarsal V of the same.
Fig. 8. Proximal (upper) articular ends of metatarsals IV and V of the same.
Fig. 9. Distal (lower) articular end of metatarsal IV of the same.
Fig. 10. Front view of metatarsal IV of *Procoptodon Pusio*, fœm.
Fig. 11. Proximal articular end of the same.
Fig. 12. Back view of distal half of the same.

All the figures are of the natural size.

IX. *On Multiple Contact of Surfaces.*

By WILLIAM SPOTTISWOODE, *M.A., Treas. R.S.*

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IN a paper "On the Contact of Quadrics with other Surfaces," published in the Proceedings of the London Mathematical Society (May 14, 1874, p. 70), I have shown that it is not in general possible to draw a quadric surface V so as to touch a given surface U in more than two points, but that a condition must be fulfilled for every additional point. The equations expressing these conditions, being interpreted in one way, show that two points being taken arbitrarily the third point of contact, if such there be, must lie on a curve the equation whereof is there given. The same formulæ, interpreted in another way, serve to determine the conditions which the coefficients of the surface U must fulfil in order that the contact may be possible for three or more points taken arbitrarily upon it; and, in particular, the degrees of these conditions give the number of surfaces of different kinds which satisfy the problem.

In another paper, "Sur les Surfaces osculatrices" (Comptes Rendus, 6 Juillet, 1874, p. 24), the corresponding conditions for the osculation of a quadric with a given surface are discussed.

In the present paper I have regarded the question in a more general way; and having shown how the formulæ for higher degrees of contact are obtained, I have developed more in detail some special cases of interest.

For the convenience of the reader, I have in § 1 briefly recapitulated the principal parts of the two papers above quoted. In § 2 I have given, at all events, a first sketch of a general theory of multiple contact with quadrics; in § 3 the particular cases of three-, four-, five-, and six-pointic contact are discussed; and in § 4 some conditions for the existence of points of four-, five-, six-branched single (*i. e.* not multiple) contact are established.

Thus far the investigation concerns the contact of quadrics only with other surfaces. The concluding part of the paper is concerned with the corresponding problem for cubics, in which case conditions of possibility do not arise for either simple or two-branched contact, but are first met with for three-branched contact. The conditions in question, with some of their consequences, are here given; but it is perhaps hardly worth while to prosecute the subject much further in this direction.

It will be observed in the course of the paper that some of the numerical results must be taken as subject to limitations to be expected from further research; but the intricate nature of the investigation will, I hope, be considered as affording some justification for submitting it thus rough-hewn to the notice of the Society.

§ 1. *Recapitulation of former Methods and Results.*

Let x, y, z, t; x_1, y_1, z_1, t_1; .. be the coordinates of the points P, P_1, .. respectively; and let

$$U=(x, y, z, t)^n=0,\ V=(x, y, z, t)^m=0, \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (1)$$

be the equations of the two surfaces whose contact is the subject of consideration. The conditions of contact may, as is well known, be written thus:

$$\left.\begin{aligned} &\partial_x U : \partial_y U : \partial_z U : \partial_t U \\ =&\partial_x V : \partial_y V : \partial_z V : \partial_t V. \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (2)$$

Another form of these conditions is, however, better adapted to our present purpose. In fact, writing

$$\left.\begin{aligned} &\partial_y V\partial_x U-\partial_x V\partial_y U=\delta U,\ \partial_z V\partial_t U-\partial_t V\partial_z U=\delta_3 U, \\ &\partial_z V\partial_x U-\partial_x V\partial_z U=\delta_1 U,\ \partial_y V\partial_t U-\partial_t V\partial_y U=\delta_4 U, \\ &\partial_z V\partial_y U-\partial_y V\partial_z U=\delta_2 U,\ \partial_x V\partial_t U-\partial_t V\partial_x U=\delta_5 U, \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad (3)$$

or, more briefly,

$$\left\| \begin{matrix} \partial_x U, & \partial_y U, & \partial_z U, & \partial_t U \\ \partial_x V, & \partial_y V, & \partial_z V, & \partial_t V \end{matrix} \right\| = \delta U, \ \delta_1 U, \ldots \delta_5 U, \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (4)$$

we may take as the conditions necessary, in order that V shall touch U at the point P, any two of the six following, viz.:

$$\delta U=0,\ \delta_1 U=0, \ldots \delta_5 U=0. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (5)$$

Similarly, as I have shown in a memoir "On the Contact of Surfaces" (Phil. Trans. 1872, p. 259), we may take as the further conditions that V (assumed to touch U at the point P) may have a three-branch contact* with V at the point P, any three independent equations of the following system:

$$\delta^2 U=0,\ \delta_1{}^2 U=0, \ldots \delta\delta_1 U=0, \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (6)$$

and so on for higher degrees of contact.

For the purpose of the present inquiry it will be convenient to transform the equations (5) and (6) into yet another shape. Thus, if we write

$$\left.\begin{aligned} &(x, y, z, t)^n=0^n,\ (x, y, z, t)^{n-1}(x_1, y_1, z_1, t_1)=0^{n-1}1, \\ &(x, y, z, t)^2=0^2,\ (x, y, z, t)\ \ (x_1, y_1, z_1, t_1)=01, \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad (7)$$

and multiply each number of the system (2), first by x_1, y_1, z_1, t_1 respectively, and add, then by x_2, y_2, z_2, t_2, and add, and so on, we shall obtain the systems

$$\left.\begin{aligned} &0^{n-1}1 : 0^{n-1}2 : \ldots \\ =\ &01\ :\ 02\ :\ \ldots \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (8)$$

* The terms 2-branch, 3-branch, &c. contact, already used by Professors Cayley and Clifford, have the following signification:—in ordinary contact the curve of intersection has at the point a double point, or two branches; in contact of the second order, a triple point, or three branches, and so on.

This result may be generalized by introducing operative symbols, as follows:—

Let $$P_{10}=x_1\partial_x+y_1\partial_y+z_1\partial_z+t_1\partial_t$$

be a differential operator, capable of operating on functions of x, y, z, t, and containing x_1, y_1, z_1, t_1 as mere constants; then

$$\square_{12} \text{ (or more completely expressed } \boxed{\circ}_{12})$$
$$=P_{10}V\,.\,P_{20}-P_{20}V\,.\,P_{10}$$

is a differential operator capable of operating on any function of x_1, y_1, z_1, t_1; x_2, y_2, z_2, t_2; in which, when V is a quadric in x, y, z, t, $P_{10}V=P_{01}V_1$. Operating with $\square_{12}$ on $U=(x, y, z, t)^n$, we have $\square_{12}V=$a function of the form

$$(x_1, y_1, z_1, t_1)(x_2, y_2, z_2, t_2)(x, y, z, t)^n,$$

linear in the coefficients of V, and also in those of U.

With this explanation we may write

$$\left.\begin{array}{ccc} 01\,.\,0^{n-1}2-02\,.\,0^{n-1}1=\square_{12}U, \\ 01\,.\,0^{n-1}3-03\,.\,0^{n-1}1=\square_{13}U, \\ \quad .. \qquad\quad .. \qquad\quad .. \\ 02\,.\,0^{n-1}3-03\,.\,0^{n-1}2=\square_{23}U, \end{array}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (9)$$

or, more briefly,

$$\left\| \begin{array}{ccc} 0^{n-1}1, & 0^{n-1}2, & .. \\ 01\ , & 02\ , & .. \end{array} \right\| = \square_{12}U,\ \square_{13}U,\ ..\ \square_{23}U, \ldots; \quad . \quad . \quad . \quad . \quad . \quad (10)$$

and the system (5) may then be replaced by the following, viz.

$$\square_{12}U=0,\ \square_{13}U=0,\ ..\ \square_{23}U=0, \ldots \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (11)$$

any two of which may be taken as the conditions required. Similarly the system (6) may be replaced by the following, viz.

$$\square_{12}^2U=0,\ \square_{13}^2U=0,\ ..\ \square_{12}\square_{13}U=0, \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (12)$$

any three independent members of which may be taken as the conditions required.

If the two surfaces touch at a second point P_1, we may form expressions similar to (10) but involving the coordinates of P_1 in the place of those of P, thus:—

$$\left\| \begin{array}{ccc} 1^{n-1}0, & 1^{n-1}2, & .. \\ 10\ , & 12\ , & .. \end{array} \right\| = \square_{02}U_1,\ \square_{03}U_1,\ ..\ \square_{23}U_1, \ldots \quad . \quad . \quad . \quad . \quad (13)$$

and the conditions for contact at the point P_1 will be comprised in the system

$$\square_{02}U_1=0,\ \square_{03}U_1=0,\ ..\ \square_{23}U_1=0. \ldots \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (14)$$

Similarly, the conditions for contact at a third point P_2 will be comprised in the system

$$\square_{01}U_2=0,\ \square_{03}U_2=0,\ ..\ \square_{13}U_2=0, \ldots \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (15)$$

and so on for any number of points.

In the same way the conditions for osculation at a second point P_1 will be comprised in the system

$$\square_{02}^{s} U_1=0, \quad \square_{03}^{s} U_1=0, \ldots \square_{02}\square_{03}U_1=0, \ldots \ldots \ldots \quad (16)$$

and so on for any number of points.

Returning to the equations (11), (14), (15), which express the conditions for contact at the three points P, P_1, P_2, and selecting a suitable member from each system, we may form the following group:

$$\square_{12}U=0, \quad \square_{20}U_1=0, \quad \square_{01}U_2=0. \ldots \ldots \ldots \quad (17)$$

These written in full are as follows:—

$$01 \,.\, 0^{s-1}2=02 \,.\, 0^{s-1}1$$
$$12 \,.\, 1^{s-1}0=10 \,.\, 1^{s-1}2$$
$$20 \,.\, 2^{s-1}1=21 \,.\, 2^{s-1}0,$$

whence, multiplying together the dexter and sinister sides of these equations respectively, and rejecting the common factor $12 \,.\, 20 \,.\, 01$, we obtain as a condition for the possibility of a quadric V touching a surface U in the three points P, P_1, P_2, the following equation:—

$$0^{s-1}1 \,.\, 1^{s-1}2 \,.\, 2^{s-1}0=0^{s-1}2 \,.\, 1^{s-1}0 \,.\, 2^{s-1}1 \ldots \ldots \ldots \quad (18)$$

This equation shows that the three points must be so situated that each lies on one of the intersections of the first polars of the other two with respect to the surface U; for it may be written in each of the following forms, viz.

$$0^{s-1}1-\lambda 0^{s-1}2=0,$$
$$1^{s-1}2-\mu 1^{s-1}0=0,$$
$$2^{s-1}0-\nu 2^{s-1}1=0.$$

In order to account geometrically for the existence of the equation of condition, we may observe, as Professor CAYLEY has remarked, that, drawing through the points P, P_1, P_2 a plane, this plane meets the three tangent-planes of the surface U in the three sides of a triangle, which sides pass respectively through the points P, P_1, P_2; and also meets the surface V in a conic touching the sides of the triangle in these points P, P_1, P_2 respectively. Considering these points as given, a relation is implied between the directions of the three sides; viz. the triangle must be such that if each summit be joined to the opposite point the three joining lines will meet in a point.

In order that contact may subsist for a fourth point P_3 we may take either the points P_1, P_2, P_3, giving as the condition

$$1^{s-1}2 \,.\, 2^{s-1}3 \,.\, 3^{s-1}1=2^{s-1}1 \,.\, 3^{s-1}2 \,.\, 1^{s-1}3 \ldots \ldots \ldots \quad (19)$$

or the points P_2, P, P_3, giving

$$2^{s-1}0 \,.\, 0^{s-1}3 \,.\, 3^{s-1}2=0^{s-1}2 \,.\, 3^{s-1}0 \,.\, 2^{s-1}3 \,. \ldots \ldots \ldots \quad (20)$$

or the points P, P_1, P_2, giving

$$0^{n-1}1\,.\,1^{n-1}3\,.\,3^{n-1}0=1^{n-1}0\,.\,3^{n-1}1\,.\,0^{n-1}3\,. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (21)$$

But since in any one of these conditions (19), (20), (21) combined with (18) will ensure contact at the four points, it follows that the four equations (18)..(21) must be equivalent to only two independent relations. It is perhaps worth while to verify this analytically. In fact, if we multiply together the dexter and sinister sides of (19), (20), (21) respectively, and reject the common factor

$$k=0^{n-1}3\,.\,1^{n-1}3\,.\,2^{n-1}3\,.\,3^{n-1}0\,.\,3^{n-1}1\,.\,3^{n-1}2,$$

we shall reproduce the equation (18). Again, if we represent the equations (19), (20), (21), (18) respectively by the following expressions,

$$a=a',\ b=b',\ c=c',\ d=d',$$

the multiplications above indicated give as their result

$$abc=a'b'c'=kd=kd';$$

and consequently if any two of the equations $a=a'$, $b=b'$, $c=c'$ be satisfied, the third, as well as the equation $d=d'$, will be so also; which is the verification required.

This, as Professor CAYLEY has pointed out, gives rise to an interesting theorem of Solid Geometry; viz. writing for greater symmetry $\alpha, \beta, \gamma, \delta$, instead of P, P_1, P_2, P_3, and considering ABCD the tetrahedron formed by the tangent planes of U at the same four points respectively, we have the tetrahedron ABCD, the planes whereof contain the points $\alpha, \beta, \gamma, \delta$, respectively. Now the plane of $\alpha\beta\gamma$ determines with the planes BCD, CDA, DAB, a triangle, the sides whereof contain the points α, β, γ, and which is such that the lines joining the summits with the opposite points meet in a point. Similarly the planes of $\beta\gamma\delta$, $\gamma\delta\alpha$, $\delta\alpha\beta$ determine three other triangles having similar properties. And the theorem is that, if the foregoing relation be satisfied for any two of the triangles, it will be satisfied for the other two.

The equation (18) may be regarded either as a relation between the coordinates of the three points P, P_1, P_2, or as a relation between the coefficients of U. In the first case it shows that if two of the points be taken arbitrarily, the third must be on a curve defined by (18) together with the equation U=0. As to the fourth point of contact, if such there be, suppose that we represent the equations (19), (20), (21), (18) by the symbols (1, 2, 3)=0, (0, 2, 3)=0, (0, 1, 3)=0, (0, 1, 2)=0; then taking arbitrarily the points P, P_1, the curve on which P_2 must lie will be given by the equation (0, 1, 2)=0. The equation (0, 1, 3)=0 merely shows that P_2 must lie on the same curve; but the equation (0, 2, 3) shows that, if P_2 be taken arbitrarily on the curve in question, P_2 will lie at one of a finite number of points on the curve. In fact, if we take $U_2=0$ as the condition that P_2 shall lie on the surface, (0, 1, 3)=0 as the equation expressing the condition that P_2 shall lie on the curve, and (0, 2, 3) the additional condition for contact at P_2, we shall have three equations each of the degree n for determining the coordinates of P_2. The number of positions for P_2 will therefore

apparently be n^3; but this number doubtless admits of some reduction in consequence of the particular form of the equations. In fact, if a, b.. be the coefficients of the highest powers of x_2, y_2,.. in the equation $S^n=0$, then the terms involving a^3, b^3,.. in (18) all vanish. But I have not as yet fully investigated this question.

Turning to the second view of the case, which is in fact the more interesting, viz. that in which (18) is to be considered as a relation between the coefficients of U, we have for every point of contact four equations, viz.

$$U=0,\quad \partial_x U : \partial_y U : \partial_z U = \partial_x V : \partial_y V : \partial_z V,\quad V=0,$$

or their equivalents; *i. e.* for p points of contact $4p$ equations, viz.

p	equations involving	the coefficients of	U alone,
$2p$	,,	,,	U & V,
p	,,	,,	V alone.

But of the $2p$ equations which involve the coefficients of U & V, $p-2$ may be cleared of those belonging to V, and reduced to the form (18); and we hence have finally

$2p-2$	equations involving	the coefficients of	U alone,
$p+2$	,,	,,	U & V,
p	,,	,,	V alone.

By means of the last $2p+2$ equations let us determine as many as possible of the coefficients of V. Then if $2p+2>9$ we shall be able to eliminate those coefficients in $2p-7$ different ways, and obtain $2p-7$ equations involving the coefficients of U to the degree $10-p$; p being supposed $\geqslant 9$. We may thence form the following table of conditions to which the surface U will be subject:—

Number of points.	Number of coefficients of V determined.	Number of conditions in U.	Numbers and degrees of conditions in coefficients of U.		
			Of degree 1.	Of degree 3.	Also
3	8	4	3	1	
4	9	7	4	2	1 of degree 6
5	9	11	5	3	3 ,, ,, 5
6	9	15	6	4	5 ,, ,, 4
7	9	19	7	5	7 ,, ,, 3
8	9	23	8	6	9 ,, ,, 2
9	9	27	9	7	11 ,, ,, 1

It must, however, be owned that these numbers, although doubtless true as superior limits, must evidently undergo some reduction after a detailed examination of the equations upon which they depend. And on this account I abstain at present from writing down the geometrical theorems which will obviously occur to the reader on perusing these results.

Thus far for simple or two pointic contact. In order to find the conditions for three-branch contact at several points, we must, as in the second paper above quoted,

employ the equations (12) and (16); and for this purpose it is necessary in the first place to develop the formula $\square^2_{13}U$; viz. we have

$$\left.\begin{aligned}\square^2_{13}U=&(02)^2 0^{n-2}1^2-2\,.\,01\,.\,02\,.\,0^{n-2}12+(01)^2 0^{n-2}2^2\\&-02\,.\,0^{n-1}2\,.\,1^2+(02\,.\,0^{n-1}1+01\,.\,0^{n-1}2)12-01\,.\,0^{n-1}1\,.\,2^2\end{aligned}\right\}\quad\ldots\quad(22)$$

But having reference to the conditions $\square_{20}U=0$, $\square_{21}U=0$, .. we may put (θ being an indeterminate quantity)

$$01=\theta 0^{n-1}1,\ 02=\theta 0^{n-1}2,\quad\ldots\ldots\ldots\quad(23)$$

whence, by substituting these values in the developed form of the equation $\square^2_{12}U=0$, and dividing throughout by θ, we obtain

$$\left.\begin{aligned}&\theta\{(0^{n-1}2)^2 0^{n-2}1^2-2\,.\,0^{n-1}1\,.\,0^{n-1}2\,.\,0^{n-2}12+(0^{n-1}1)^2 0^{n-2}2^2\}\\&=(0^{n-1}2)^2 1^2-2\,.\,0^{n-1}1\,.\,0^{n-1}2\,.\,12+(0^{n-1}1)^2 2^2\}\end{aligned}\right\}\quad\ldots\quad(24)$$

But since P_1, P_2 are supposed to lie on the quadric V, we have $1^2=0$, $2^2=0$; so that the equation last above written is reduced to the following, viz.

$$2\,.\,0^{n-1}1\,.\,0^{n-1}2\,.\,12=-\theta\{(0^{n-1}2)^2 0^{n-2}1^2-\ldots\}=\theta\begin{vmatrix}.&0^{n+1}1,&0^{n-1}\,2\\0^{n-1},&0^{n-2}1^2,&0^{n-2}12\\0^{n-1}2,&0^{n-2}21,&0^{n-2}\,2^2\end{vmatrix},$$

or, as this may be written for greater symmetry,

$$\begin{aligned}&=\theta\begin{vmatrix}0^{n-2}\,0^2,&0^{n-2}01,&0^{n-2}02\\0^{n-2}10,&0^{n-2}\,1^2,&0^{n-2}12\\0^{n-2}20,&0^{n-2}21,&0^{n-2}\,2^2\end{vmatrix}\\&=\theta\,[0',1,2]\text{ suppose};\end{aligned}$$

and one expression for three-branched contact at the point P will be

$$2\,.\,0^{n-1}1\,.\,0^{n-1}2\,.\,12=\theta[0',1,2].$$

A similar transformation may be applied to $\square^2_{13}U$, ..; and also to $\square_{12}\square_{13}U$, ..; but the latter forms, which are rather more complicated, are not necessary for the present purpose. This being so, if the surfaces touch at the four points P, P_1, P_2, P_3, we may take for the conditions of osculation at the point P the three equations $\square^2_{23}U=0$, $\square^2_{31}=0$, $\square^2_{12}U=0$, which being transformed in the manner above explained give the following results, viz.:—

$$\left.\begin{aligned}&2\,.\,0^{n-1}2\,.\,0^{n-1}3\,.\,23=\theta[0',2,3]\\&2\,.\,0^{n-1}3\,.\,0^{n-1}1\,.\,31=\theta[0',3,1]\\&2\,.\,0^{n-1}1\,.\,0^{n-1}2\,.\,12=\theta[0',1,2]\end{aligned}\right\};\quad\ldots\ldots\quad(25)$$

whence, eliminating the indeterminate quantity θ, we obtain

$$23:31:12=0^{n-1}1[0',2,3]:0^{n-1}2[0',3,1]:0^{n-1}3[0',1,2].$$

We also obtain

$$(\theta=)\frac{0^{n-1}1}{01}=\frac{0^{n-1}2}{02}=\frac{0^{n-1}3}{03}$$

$$=\frac{2.0^{n-1}2.0^{n-1}3.23}{[0',2,3]}$$

$$=\frac{2.0^{n-1}3.0^{n-1}1.31}{[0',3,1]}$$

$$=\frac{2.0^{n-1}1.0^{n-1}2.12}{[0',1,2]},$$

which are the five conditions in order that U, assumed to pass through P, and also through P_1, P_2, P_3, may have a three-branch contact at P.

Similarly for three-branched contact at the point P, we should find

$$30:02:23=1^{n-1}2[1',3,0]:1^{n-1}3[1',0,2]:1^{n-1}0[1',2,3],$$

and for osculation at the point P_3,

$$30:01:13=2^{n-1}1[2',30]:2^{n-1}3[2',0,1]:2^{n-1}0[2',1,3].$$

Substituting from these equations the values of 30 : 23, 13 : 30, 23 : 31 in the identical equation

$$(30:23)(13:30)(23:31)=1,$$

we obtain the following relation,

$$1^{n-1}2[1',3,0]2^{n-1}0[2',1,3]0^{n-1}1[0',2,3]$$
$$=1^{n-1}0[1',2,3]2^{n-1}1[2',3,0]0^{n-1}2[0',3,1],$$

which, in virtue of the condition (18), may be reduced to the form

$$[0',2,3][1',3,0][2',1,3]=[0',3,1][1',2,3][2',3,0]. \quad . \quad . \quad . \quad . \quad (26)$$

This therefore is a condition which, in addition to those found before, must be fulfilled in order that it may be possible to draw through four points P, P_1, P_2, P_3 a quadric surface which will touch the surface U in those points, and have three-branched contact with it in three of them.

The total number of conditions for two-branched contact at four points, and three-branched at one of them, may be calculated as follows:—For three-branched contact at three points we shall have the following numbers of equations in the coefficients:

3	equations	in U of the degree 1,
1	„	„ 3,
1	„	„ 9,
5	„	U and V of the degrees in U, 1; in V, 1,
8	„	„ „ 1; „ 2,
3	„	V of the degree 1.

Beside this we shall have for the two-branched contact at the fourth point, one equation in U of the degree 1, one of the degree 3, one in U and V of the degrees 1, 1, and one in V of the degree 1; so that the total number will be

4	equations in U of the degree 1,			(a)
2	„	„	3,	(b)
1	„	„	9,	(c)
6	„	U and V of the degrees in U, 1; in V, 1,		(d)
8	„	„	„ 1; „ 2,	(e)
4	„	V of the degree 1.		(f)

Taking any five of the equations marked (d) and the four marked (f), we see that all the coefficients of the quadric surface are determinate and unique; also that the quantities to which they are severally proportional are apparently of the degree 6 in the coefficients of U. Subject to future reduction of this number, the equations of condition in the coefficients of U and their degrees will be,

4	of the	degree	1,
2	„	„	3,
1	„	„	7,
1	„	„	9,
8	„	„	13.

But having these ulterior reductions of degree in view, I at present abstain from enunciating the geometrical theorems which these results suggest.

§ 2. *General Theory of Multiple Contact of Quadrics with other Surfaces.*

The question may be considered from rather a more general point of view. Dropping, for the moment, the suffixes, and taking the symbol $\square$ to represent any of the operations $\square_{12}$, $\square_{13}$, .. (say $\square_{12}$), let $\square'$ represent that part of $\square$ which operates on U, and $\square''$ that part which operates on V; so that we may write symbolically $\square = \square' + \square''$. It is first required to find the values of $\square U$, $\square^2 U$, .. in terms of $\square' U$, $\square'' U$, .. The transformation will perhaps be better understood by examining two or three special instances before entering upon the general case. Thus

$$\left.\begin{aligned} \square U &= \square' U, \\ \square^2 U &= \square'^2 U + \square'' \square' U, \\ \square^3 U &= \square'^3 U + \square'' \square'^2 U + \square' \square'' \square' U + \square''^2 \square' U. \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad (1)$$

But it will be found on developing the expression that $\square''^2 \square' U = (12)^2 \square' U$; so that if, as is supposed in the present problem, the two surfaces touch at the point under consideration (a condition which is expressed by the equation $\square' U = 0$), we have always

$\square''^{3}\square'U=0$. Moreover

$$\begin{aligned}\square'\square''\square'U &= n(12)\square'^{2}(02\,.\,0^{n-1}1+01\,.\,0^{n-1}2)\\ &= n(n-1)(12)\{(02)^{2}0^{n-2}1^{2}-(01)^{2}0^{n-2}2^{2}\},\\ \square''\square'^{2}U &= n(n-1)\square''\{(02)^{2}0^{n-2}1^{2}-2\,.\,01\,.\,02\,.\,0^{n-2}12+(01)^{2}0^{n-2}2^{2}\}\\ &= 2n(n-1)(12)\{(02)^{2}0^{n-2}1^{2}-(01)^{2}0^{n-2}2^{2}\};\end{aligned}$$

so that we have generally the relation

$$\square'\square''\square'U=\tfrac{1}{2}\square''\square'^{2}U,$$

and consequently

$$\square'^{2}U=\square'^{2}U+\tfrac{2}{3}\square''\square'^{2}U. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (2)$$

Proceeding to the fourth degree, we obtain, by means of the formulæ already established, the following expression:—

$$\square'^{4}U=\square'^{4}U+\square''\square'^{3}U+\tfrac{3}{2}\square'\square''\square'^{2}U+\tfrac{2}{3}\square''^{2}\square'^{2}U.$$

But operating with $\square'$ on the expression given above for $\square''\square'^{2}U$, we obtain

$$\begin{aligned}\tfrac{3}{2}\square'\square''\square'^{2}U=3n(n-1)(n-2)(12)\{&(02)^{2}0^{n-3}1^{2}-01(02)^{2}0^{n-3}1^{2}2\\ &-(01)^{2}02\,.\,0^{n-3}12^{2}+(01)^{2}0^{n-3}2^{2}\};\end{aligned}$$

also

$$\begin{aligned}\square''^{2}U = n(n-1)(n-2)\ \{&(02)^{2}0^{n-3}1^{2}-3(02)^{2}01\,.\,0^{n-3}1^{2}2\\ &+3(01)^{2}02\,.\,0^{n-3}12^{2}-(01)^{2}0^{n-3}2^{2}\}.\end{aligned}$$

Hence, operating upon this with $\square''$, we should find

$$\tfrac{3}{2}\square'\square''\square''^{2}U=\square''\square''^{2}U;$$

and consequently, collecting the former results,

$$\begin{aligned}\square U &= \square'U,\\ \square^{2}U &= \square'^{2}U+\square''\square'U,\\ \square^{3}U &= \square'^{3}U+\tfrac{2}{3}\square''\square'^{2}U,\\ \square^{4}U &= \square'^{4}U+\tfrac{4}{3}\square''\square'^{3}U+\tfrac{2}{3}\square''^{2}\square'^{2}U. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (3)\end{aligned}$$

Having now seen, in the special cases $m=2, 3, 4$, the nature of the transformations contemplated, we may now proceed to the more general case; viz. since the order of the operations $\square'$, $\square''$ is not indifferent, we have in general for $\square^{m}U$ an expression of the form

$$\begin{aligned}\square^{m}U=&\square'^{m}U\\ &+\square''\square'^{m-1}U+\square'\square''\square'^{m-2}U+\,.\,.\\ &+\square''^{2}\square'^{m-2}U+\square''\square'\square''\square'^{m-3}U+\,.\,.\\ &+\,.\,.; \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (4)\end{aligned}$$

and our first object is to show how this may be reduced to the form

$$A\square'^{m}U+B\square''\square'^{m-1}U+C\square''^{2}\square'^{m-2}U+\,.\,.\,A'\square'^{m-3}U+\,.\,.$$

Now the general term of $\square'^{m}U$ is

$$n(n-1)\,..\,(n-m+1)(-)^i\frac{m(m-1)\,..\,(m-i+1)}{1\,.\,2\,..\,i}(02)^{m-i}(01)^i0^{n-m}1^{m-i}2^i;$$

and it will be found on examination that the general term of $\square''\square'^{m}U$ differs from that of $\square'^{m}U$ only in respect of the factor $(12)(m-2i)$. Similarly the general terms of $\square'''\square'^{m}U, \,..\, \square''^{p}\square'^{m}U$ differ from that of $\square'^{m}U$ only in respect of the factors $(12)^2(m-2i)^2, \,..\, (12)^p(m-2i)^p$, respectively.

This being so, let $\delta_1=x_1\partial_x+\,..\,, \delta_2=x_2\partial_x+\,..\,$; and let it be understood that δ_1, δ_2 affect the external subject of operation alone, then we may write

$$\square'^{m}U=(02\delta_1-01\delta_2)^mU;$$

and if we write the above expression in the form of a quantic, thus,

$$\square'^{m}U=(1, 1, \,..\,)(02\delta_1, -01\delta_2)^mU,$$

we may at once write down the expression for $\square''^{p}\square'^{m}U$ thus,

$$(12)^p(m^p, (m-2)^p, (m-4)^p, \,..\,)(02\delta_1, -01\delta_2)^mU. \quad . \quad . \quad . \quad . \quad . \quad (5)$$

Having thus exhibited the form of the function $\square''^{p}\square'^{m}U$, we must next calculate the effect of the operation $\square'$ upon this function; and if for this purpose we operate with $\square'$ upon the general term of $\square''^{p}\square'^{m}U$, we shall find for the general term of $\square'\square''^{p}\square'^{m}U$ the following expression:—

$$n(n-i)\,..\,(n-m)(-)^i(12)^p\left\{\begin{array}{l}\dfrac{m(m-1)\,..\,(m-i+1)}{1\,.\,2\,..\,i}(m-2i)^p\\ +\dfrac{m(m-1)\,..\,(m-i+2)}{1\,.\,2\,..\,(i-1)}(m-2i+2)^p\end{array}\right\}(02)^{m-i+1}(01)^i0^{n-m-1}1^{m-i+1}2^i$$

$$=n(n-1)\,..\,(n-m)(-)^i(12)^p\frac{m(m-1)\,..\,(m-i+1)}{1\,.\,2\,..\,i}$$

$$\{(m-i+1)(m-2i)^p+i(m-2i+2)^p\}(02)^{m-i+1}(01)^i0^{n-m-1}1^{m-i+1}2^i.$$

As regards the coefficient between the brackets $\{\ \}$, let $m-2i+1=\mu$; then for $p=1, 2, \,..$ we have successively

$$(m-i+1)(\mu-1)+i(\mu+1)=m\mu,$$

$$(m-i+1)(\mu-1)^2+i(\mu+1)^2=(m+1)\mu^2-2\mu^2+(m+1)$$
$$=(m-1)\mu^2+(m+1),$$

$$(m-i+1)(\mu-1)^3+i(\mu+1)^3=(m+1)\mu^3-3\mu^3+3(m+1)\mu-\mu$$
$$=(m-2)\mu^3+(3m+2)\mu,$$

$$(m-i+1)(\mu-1)^4+i(\mu+1)^4=(m+1)\mu^4-4\mu^4+6(m+1)\mu^2-4\mu^2+(m+1)$$
$$=(m-3)\mu^4+2(3m+1)\mu^2+(m+1);$$

and generally

$$(m-i+1)(\mu-1)^p+i(\mu+1)^p=(m-p+1)\mu^p$$
$$+\frac{p(p-1)}{1.2.3}(3m-p+5)\mu^{p-2}$$
$$+\frac{p(p-1)(p-2)(p-3)}{1.2.3.4.5}(5m-p+9)\mu^{p-4}$$
$$+\ldots$$
$$+\frac{p(p-1)\ldots(p-j+2)}{1.2\ldots j}(jm-p+2j-1)\mu^{p-j+1}$$
$$+\ldots,$$

in which it is to be understood that j is always an odd number.

From these transformations we obtain the following results, viz.:—

$$\left.\begin{aligned}
&\square'\square''\square'^{m}\mathrm{U}=\frac{m}{m+1}\square''\square'^{m+1}\mathrm{U},\\
&\square'\square''^{2}\square'^{m}\mathrm{U}=\frac{m-1}{m+1}\square''^{2}\square'^{m+1}\mathrm{U}+(12)^{2}\square'^{m+1}\mathrm{U},\\
&\square'\square''^{3}\square'^{m}\mathrm{U}=\frac{m-2}{m+1}\square''^{3}\square'^{m+1}\mathrm{U}+(12)^{2}\frac{3m+2}{m+1}\square''\square'^{m+1}\mathrm{U},\\
&\quad\ldots\qquad\ldots\\
&\square'\square''^{p}\square'^{m}\mathrm{U}=\frac{m-p+1}{m+1}\square''^{p}\square'^{m+1}\mathrm{U}+\frac{p(p-1)}{1.2.3}\frac{3m-p+5}{m+1}(12)^{2}\square''^{p-2}\square'^{m+1}\mathrm{U}+\ldots\\
&\qquad+\frac{p(p-1)\ldots(p-j+2)}{1.2\ldots j}\frac{jm-p+2j-1}{m+1}(12)^{j-1}\square''^{p-j+1}\square'^{m+1}\mathrm{U}+\ldots
\end{aligned}\right\}\quad(6)$$

But since the general term of the expansion of $\square^{m}\mathrm{U}$ will be of the form $\square''^{\beta}\square'^{\beta}\square''^{\alpha}\square'^{\alpha}\mathrm{U}$, it follows from these formulæ that every such term, and consequently the whole expansion, may by successive steps be reduced to a series of terms of the form $\square''^{p-s}\square'^{m-p}\mathrm{U}$.

Before proceeding further with the main question it will be worth while to notice a few consequences of these reductions. Thus, in the first place,

$$\square'^{2}\square''\square'^{m}\mathrm{U}=\frac{m}{m+1}\square'\square''\square'^{m+1}\mathrm{U}=\frac{m}{m+1}\cdot\frac{m+1}{m+2}\square''\square'^{m+2}\mathrm{U};$$

whence we obtain the following system:—

$$\left.\begin{aligned}
&\square'\,\square''\square'^{m}\mathrm{U}=\frac{m}{m+1}\square''\square'^{m+1}\mathrm{U},\\
&\square'^{2}\square''\square'^{m}\mathrm{U}=\frac{m}{m+2}\square''\square'^{m+2}\mathrm{U},\\
&\square'^{3}\square''\square'^{m}\mathrm{U}=\frac{m}{m+3}\square''\square'^{m+3}\mathrm{U},\\
&\quad\ldots\qquad\ldots\\
&\square'^{m_1}\square''\square'^{m}\mathrm{U}=\frac{m}{m+m_1}\square''\square'^{m+m_1}\mathrm{U}.
\end{aligned}\right\}\quad\ldots\ldots\ldots\quad(7)$$

Again,

$$\Box'^2\Box''^2\Box'^m\mathrm{U}=\Box'\left\{\frac{m-1}{m+1}\Box''^3\Box'^{m+1}\mathrm{U}+(12)^3\Box'^{m+1}\mathrm{U}\right\}$$

$$=\frac{m(m-1)}{(m+2)(m+1)}\Box''^2\Box'^{m+2}\mathrm{U}+(12)^3\left(\frac{m-1}{m+1}+1\right)\Box'^{m+2}\mathrm{U};$$

whence the system

$$\left.\begin{aligned}\Box'^2\Box''^2\Box'^m\mathrm{U}&=\frac{m(m-1)}{(m+2)(m+1)}\Box''^2\Box'^{m+2}\mathrm{U}+\frac{2m}{m+1}(12)^3\Box'^{m+2}\mathrm{U},\\ \Box'^2\Box''^3\Box'^m\mathrm{U}&=\frac{m(m-1)}{(m+3)(m+2)}\Box''^2\Box'^{m+2}\mathrm{U}+\frac{3m}{m+2}(12)^3\Box'^{m+2}\mathrm{U},\\ \cdots&\qquad\cdots\end{aligned}\right\}\quad\ldots\quad(8)$$

Assuming this to be true for m_1-1, we should have

$$\Box'^{m_1-1}\Box''^2\Box'^m\mathrm{U}=\frac{m(m-1)}{(m+m_1-1)(m+m_1-2)}\Box''^2\Box'^{m+m_1-1}\mathrm{U}+\frac{(m_1-1)m}{m+m_1-2}(12)^3\Box'^{m+m_1-1};$$

then operating again with $\Box'$, we obtain

$$\Box'^{m_1}\Box''^2\Box'^m\mathrm{U}=\frac{m(m-1)}{(m+m_1-1)(m+m_1-2)}\Box''^2\Box'^{m+m_1}\mathrm{U}$$

$$+\left\{\frac{m(m-1)}{(m+m_1-1)(m+m_1-2)}+\frac{(m_1-1)m}{m+m_1-2}\right\}(12)^3\Box'^{m+m_1}\mathrm{U},$$

and the numerator of the expression within the brackets

$$=m(m-1+mm_1-m+m_1^2-2m_1+1)$$

$$=m_1m(m+m_1-2);$$

so that the expression sought finally becomes

$$\frac{m(m-1)}{(m+m_1-1)(m+m_1-2)}\Box''^2\Box'^{m+m_1}\mathrm{U}-\frac{m_1m}{m+m_1-1}(12)^3\Box'^{m+m_1}\mathrm{U},\quad\ldots\quad(9)$$

which proves the law.

Once more, operating with $\Box'$ upon the expression given above for $\Box'\Box''^3\Box'^m\mathrm{U}$, we obtain

$$\Box'^2\Box''^3\Box'^m\mathrm{U}=\frac{m-2}{m+1}\left\{\frac{m-1}{m+2}\Box''^3\Box'^{m+2}\mathrm{U}+\frac{3m+5}{m+2}(12)^3\Box''\Box'^{m+2}\mathrm{U}\right\}$$

$$+\frac{3m+2}{m+1}\cdot\frac{m+1}{m+2}(12)^3\Box''\Box'^{m+2}\mathrm{U};$$

whence the system

$$\left.\begin{aligned}\Box'^3\Box''^3\Box'^m\mathrm{U}&=\frac{(m-1)(m-2)}{(m+2)(m+1)}\qquad\Box''^2\Box'^{m+3}\mathrm{U}+\frac{2(3m^2+2m-4)}{(m+2)(m+1)}\qquad(12)^3\Box''\Box'^{m+3}\mathrm{U},\\ \Box'^3\Box''^3\Box'^m\mathrm{U}&=\frac{m(m-1)(m-2)}{(m+3)(m+2)(m+1)}\Box''^2\Box'^{m+3}\mathrm{U}+\frac{3m(3m^2+5m-6)}{(m+3)(m+2)(m+1)}(12)^3\Box''\Box'^{m+3}\mathrm{U},\\ \Box'^4\Box''^3\Box'^m\mathrm{U}&=\frac{m(m-1)(m-2)}{(m+4)(m+3)(m+2)}\Box''^3\Box'^{m+4}\mathrm{U}+\frac{4m(3m^2+8m-8)}{(m+4)(m+3)(m+2)}(12)^3\Box''\Box'^{m+4}\mathrm{U}.\\ \cdots&\qquad\cdots\end{aligned}\right\}\quad(10)$$

Assuming this to be true for m_1-1, we should have

$$\square'^{m_1-1}\square''^{m}\square'^{m}\mathrm{U}=\frac{m(m-1)(m-2)}{(m+m_1-1)(m+m_1-2)(m+m_1-3)}\square''^{m}\square'^{m+m_1-1}\mathrm{U}$$
$$+\frac{(m_1-1)m\{3m^2+(3m_1-7)m-2m_1+2\}}{(m+m_1-1)(m+m_1-2)(m+m_1-3)}(12)^2\square''\square'^{m+m_1-1}\mathrm{U};$$

then operating with $\square'$ we obtain

$$\square'^{m_1}\square''^{m}\square'^{m}\mathrm{U}=\frac{m(m-1)(m-2)}{(m+m_1-1)(m+m_1-2)(m+m_1-3)}\left\{\frac{m+m_1-3}{m+m_1}\square''^{m}\square'^{m+m_1}\mathrm{U}\right.$$
$$\left.+\frac{3m+3m_1-1}{m+m_1}(12)^2\square''\square'^{m+m_1}\mathrm{U}\right\}$$
$$+\frac{(m_1-1)m\{(3m^2+3m_1-7)m-2m_1+2\}}{(m+m_1-1)(m+m_1-2)(m+m_1-3)}\frac{m+m_1-1}{m+m_1}(12)^2\square''\square'^{m+m_1}\mathrm{U}$$
$$=\frac{m(m-1)(m-2)}{(m+m_1)(m+m_1-1)(m+m_1-2)}\square''^{m}\square'^{m+m_1}\mathrm{U}$$
$$+\frac{m}{(m+m_1)(m+m_1-1)(m-m_1-2)}\frac{1}{(m+m_1-3)}(12)^2\square''\square'^{m+m_1}\mathrm{U}$$
$$\{(m-1)(m-2)(3m+3m_1-1)+(m_1-1)(3m^2+3mm_1-7m-2m_1+2)(m+m_1-1)\};$$

and the quantity within the brackets $\{\ \}$

$$=3m_1(m-1)(m-2)+(3m-1)(m-1)(m-2)$$
$$+\{m_1(3m-2)+(3m-1)(m-2)\}\{m_1(m_1+m-2)-(m-1)\},$$

of which the part independent of m_1 obviously vanishes, and the remainder

$$=m_1\{3(m-1)(m-2)+m_1(3m-2)(m_1+m-2)-(3m-2)(m-1)+(3m-1)(m-2)(m_1+m-2)\};$$

or if we put $m+m_1-3=\mu$, $m+m_1-2=\mu+1$, $m_1=\mu-(m-3)$, the above expression becomes

$$=m_1\{3(m-1)(m-2)+(\mu-m+3)(3m-2)(\mu+1)-(3m-2)(m-1)+(3m-1)(m-2)(\mu+1)\}$$
$$=m_1\{3(m-1)(m-2)-(m-3)(3m-2)-(3m-2)(m-1)+(3m-1)(m-2)$$
$$+\mu[-(3m-2)(m-4)+(3m-1)(m-2)]+\mu^2(3m-2)\}$$
$$=m_1(m+m_1-3)\{(m+m_1-3)(3m-2)+7m-6\}$$
$$=m_1(m+m_1-3)\{3m^2+(3m_1-4)m+2m_1\};$$

so that the expression for the value of $\square'^{m_1}\square''^{m}\square'^{m}\mathrm{U}$ finally becomes

$$\left.\begin{aligned}&\frac{m(m-1)(m-2)}{(m+m_1)(m+m_1-1)(m+m_1-2)}\square''^{m}\square'^{m+m_1}\mathrm{U}\\&+\frac{m_1m\{3m^2+(3m_1-4)m+2m_1\}}{(m+m_1)(m+m_1-1)(m+m_1-2)}(12)^2\square''\square'^{m+m_1}\mathrm{U},\end{aligned}\right\}\quad\ldots\ldots\quad(11)$$

which proves the law.

It seems unnecessary to pursue these developments further.

It has now been shown that the expression for $\Box^m$ may be reduced to the form

$$\Box'^m+\beta\Box''\Box'^{m-1}+(\gamma\Box'^3+\gamma'\Box'')\Box'^{m-3}+\ldots(\Sigma_r\kappa\Box'^{m-r})\Box'^r.$$

Hence, on replacing each term of this series by its value given by (5), we find that the expression for $\Box^m U$ may ultimately be reduced to the form

$$\{A(02\partial_1, -01\partial_2)^m+B(12)(02\partial_1, -01\partial_2)^{m-1}+\ldots K(12)^{m-2}(02\partial_1, -01\partial_2)^2\}U, \quad (12)$$

or, still more symbolically,

$$(A, B, \ldots K)((02\partial_1, -01\partial_2), (12))^{m-2}(02\partial_1, -01\partial_2)^2U,$$

excepting in the case of $m=2$, when there is one extra term, as was seen at the outset and as will be noticed again below. This being so, we may eliminate the quantities 01, 02 by the formulæ $01=\theta 0^{n-1}1$, $02=\theta 0^{n-1}2$, and then divide out θ^2 throughout. The expression is then reduced to the following form,

$$(A, B, \ldots K)(\theta(0^{n-1}2\partial_1, -0^{n-1}1\partial_2), (12))^{m-2}(0^{n-1}2\partial_1, -0^{n-1}1\partial_2)^2U.$$

But if the surfaces touch at either of the points P_1, P_2 (say P_1), we shall have

$$12=\theta_1 1^{n-1}2, \quad \theta=\frac{01}{0^{n-1}1}=\frac{1^{n-1}0}{0^{n-1}1}\theta_1,$$

or

$$\theta : 1^{n-1}0=12 : 0^{n-1}1\,.\,1^{n-1}2; \quad \ldots\ldots\ldots\ldots \quad (13)$$

so that the expression in question may be finally cleared of all quantities relating to the quadric V (01, 02, 12), and reduced to the form

$$(A, B, \ldots K)(1^{n-1}0(0^{n-1}2\partial_1, -0^{n-1}\partial_2), \ 0^{n-1}1\,.\,1^{n-1}2)^{m-2}(0^{n-1}2\partial_1, -0^{n-1}1\partial_2)^2U, \quad (14)$$

in which it is to be remembered that ∂_1, ∂_2 operate only on the external subject U, and not upon any of its derivatives occurring in the operative factors themselves.

It is in the eliminations effected by means of the formula (13) that the main difference between the methods of this and of the former papers consists. The conditions for multiple contact here established are more numerous, and at the same time of lower degrees, and therefore more stringent, than those found before; but they appear to carry the subject to its limit.

If the surfaces touch also at the point P_2, we may in like manner use as the formulæ for elimination the following, viz.

$$21=\theta_2 2^{n-1}1, \quad \theta=\frac{02}{0^{n-1}2}=\frac{2^{n-1}0}{0^{n-1}2}\theta_2.$$

The results obtained by these two methods cannot of course be independent. In fact the equivalence of the two forms may be readily shown as follows. The first result is a rational function, homogeneous in the two quantities $1^{n-1}0$, $0^{n-1}1\,.\,1^{n-1}2$, say

$$(1^{n-1}0, \ 0^{n-1}1\,.\,1^{n-1}2)^{m-2}=0;$$

and in like manner the second may be represented by the equation

$$(2^{n-1}0, \ 0^{n-1}2\,.\,2^{n-1}1)^{m-2}=0.$$

On multiplying the first by $(2^{s-1}0)^{m-s}$, and the second by $(1^{s-1}0)^{m-s}$, we obtain the two expressions

$$(1^{s-1}0\,.\,2^{s-1}0,\ 0^{s-1}1\,.\,1^{s-1}2\,.\,2^{s-1}0)^{m-s}=0,$$
$$(1^{s-1}0\,.\,2^{s-1}0,\ 0^{s-1}2\,.\,2^{s-1}1\,.\,1^{s-1}0)^{m-s}=0.$$

But since the surfaces touch in the three points P, P_1, P_2, it follows that

$$0^{s-1}1\,.\,1^{s-1}2\,.\,2^{s-1}0=0^{s-1}2\,.\,2^{s-1}1\,.\,1^{s-1}0.$$

Hence the two expressions are equivalent.

It is further to be noticed that the last term of the expression is of the form

$$\{(02)^m\partial_1^m\pm(02)^m\partial_2^m\}\,U,$$

according as m is even or odd. Consequently from $m=5$ and upwards the last term of $\square^m U$ may always be eliminated by means of the expression for $\square^{m-2}U$; and the equation finally depressed by one degree in θ and (12).

The expression (14) when equated to zero will form one condition, which must be satisfied, either by the coordinates of the points, or by the coefficients of U, in order that it may be possible to draw a quadric having $(m+1)$-pointic contact with U at the point P_2 and contact of the same or of lower degrees at other points P_1, P_2, ...

Such is the general theory; but the subject will perhaps become more easily intelligible by the aid of the next section, in which the cases of $m=2, 3, 4, 5$ are examined in some detail.

It will probably have been remarked that we have here developed only expressions of the form $\square^m U$, and have taken no account of those of the form $\square^p_{12}\square^q_{13}U$. But the latter, which would have been more complicated, are happily unnecessary; since the eliminations above indicated will be always possible for expressions of the form $\square^m_{ij}U=0$, provided only that one of the subscript numbers shall always correspond with that of one of the points at which contact takes place. And this may always be ensured, because in all the investigations of this paper, except those contained in § 4, contact, two-pointic at least, is supposed to subsist at more than one point. Thus, if there be contact at a second point P_1, we may use the operators $\square_{12}$, $\square_{13}$, ..; if there be contact also at P_2, we may use also the operators $\square_{23}$, $\square_{24}$, ..; and so on for any number of points.

§ 3. *Conditions for the cases* $n=3, 4, 5, 6$.

With a view to examining more in detail the cases of $m=1, 2, 3, 4, 5$, we may write down the developments indicated in the preceding section thus:—

$$\left.\begin{aligned}
&\square\,U=(02\partial_1-01\partial_2)\,U,\\
&\square^2U=(02\partial_1-01\partial_2)^2U+\ (12)(02\,\partial_1+01\,\partial_2)U,\\
&\square^3U=(02\partial_1-01\partial_2)^3U+3(12)(\overline{02}^2\partial_1^2-\overline{01}^2\partial_2^2)U,\\
&\square^4U=(02\partial_1-01\partial_2)^4U+2(12)(3,\,1,\,-1,\,-3)(02\partial_1,-01\partial_2)^3U+6(12)^2(\overline{02}^3\partial_1^2+\overline{01}^3\partial_2^2)U
\end{aligned}\right\}(1)$$

Again, operating with $\square = \square' + \square''$ upon the expression for $\square^4 U$ in terms of $\square'$, $\square''$, we obtain

$$\begin{aligned}\square^4 U &= \square'^2 U + \square'' \square'^4 U + 2\square' \square'' \square'^3 U + 2\square'^2 \square'^3 U + \tfrac{3}{2}\square' \square'^2 \square'^2 U + \tfrac{3}{2}\square''^3 \square'^2 U \\ &= \square'^2 U + \tfrac{3}{2}\square'' \square'^4 U + \tfrac{5}{2}\square'^3 \square'^3 U + \tfrac{3}{2}\square'^3 \square'^2 U + \tfrac{3}{4}(12)^2 \square'^2 U.\end{aligned}$$

But

$$\begin{aligned}\square'' \square'^4 U &= (12)(4, 2, 0, -2, -4)(02\delta_1, -01\delta_2)^4 U \\ &= 2(12)(2, 1, 0, -1, -2)(02\delta_1, -01\delta_2)^4 U, \\ \square'^3 \square'^3 U &= (12)^3 (9, 1, 1, 9)(02\delta_1, -01\delta_2)^3 U, \\ \square'^3 \square'^2 U &= (12)^3 2^2 (\overline{02}^2 \delta_1^2 - \overline{01}^2 \delta_2^2) U,\end{aligned}$$

which, in virtue of the condition $\square^3 U = 0$,

$$= -(12)^2 \frac{2^2}{3}(02\delta_1 - 01\delta_2)^3 U;$$

hence

$$\begin{aligned}\square^4 U &= (02\delta_1 - 01\delta_2)^4 U \\ &\quad + 10(12)(1, 2, 0, -2, -1\tfrac{5}{7})(02\delta_1, -01\delta_2)^4 U \\ &\quad + 1\tfrac{5}{7}(12)^2 (3, 1, 1, 3\tfrac{5}{7})(02\delta_1, -01\delta_2)^2 U \\ &\quad - 4(12)^2 (02\delta_1 - 01\delta_2)^2 U \\ &\quad + \tfrac{3}{7}(12)^2 (02\delta_1 - 01\delta_2)^2 U.\end{aligned}$$

But collecting the terms of the third degree, we have for the coefficient of $(12)^2$

$$\begin{aligned}&\{(\tfrac{1}{2}\cdot 3 - 4 + \tfrac{3}{2})(02)^2 \delta_1^2 + (-\tfrac{1}{2}\cdot 5 + 12 - \tfrac{3}{2}\cdot 3)(02)^2 (01) \delta_1^2 \delta_2 + \ldots\} U \\ &= 20\left((02)^2 \delta_1^2 - (01)^2 \delta_2^2\right) U;\end{aligned}$$

so that, finally,

$$\left.\begin{aligned}\square^4 U &= (02\delta_1 - 01\delta_2)^4 U \\ &\quad + 10(12)(1, 2, 0, -2, -3\tfrac{5}{7})(02\delta_1, -01\delta_2)^4 U \\ &\quad + 20(12)^2 \left((02)^2 \delta_1^2 - (01)^2 \delta_2^2\right) U,\end{aligned}\right\} \quad \ldots \quad (2)$$

which, for greater symmetry, may be written thus:—

$$\begin{aligned}&(1, 5, 10, 10, 5, 1\tfrac{5}{7})(02\delta_1 - 01\delta_2)^5 \\ &+ 10(12)(1, 2, 0, -2, -1\tfrac{5}{7})(02\delta_1 - 01\delta_2)^4 \\ &+ 20(12)^2 (1, 0, 0, 1\tfrac{5}{7})(02\delta_1 - 01\delta_2)^3.\end{aligned}$$

These expressions may be rendered somewhat more compact by writing as follows:—

$$\left.\begin{aligned}A &= 0^{n-1} 2\delta_1 - 0^{n-1} \delta_2, \\ B &= 0^{n-1} 2\delta_1 + 0^{n-1} \delta_2;\end{aligned}\right\} \quad \ldots \quad (3)$$

and referring to the developments given above it will be found that

$$\left.\begin{aligned}
\square^2 U &= \theta A^2 U + (12)BU,\\
\square^3 U &= \theta A^3 U + (12)BAU,\\
\square^4 U &= \theta^2 A^4 U + 6\theta(12)BA^2 U + 3(12)^2(A^2+B^2)U,\\
\square^5 U &= \theta^2 A^5 U + 10\theta(12)BA^3 U + 5(12)^2(A^3+3B^2)U.
\end{aligned}\right\} \quad \ldots\ldots \quad (4)$$

For three-branch contact at P the number of equations, in addition to those for ordinary contact, is three; and replacing the suffixes, we may take for these equations the following,

$$\square^2_{13} U = 0,\ \square^2_{13} U = 0,\ \square^2_{14} = 0;$$

or, transforming as above,

$$\left.\begin{aligned}
\theta A^2_{13} U + (12)B_{13} U &= 0,\\
\theta A^2_{13} U + (13)B_{13} U &= 0,\\
\theta A^2_{14} U + (14)B_{14} U &= 0.
\end{aligned}\right\} \quad \ldots\ldots\ldots\ldots \quad (5)$$

Now since the surfaces are supposed to touch at the point P, we shall have

$$\theta = 01 : 0^{n-1}1 = 02 : 0^{n-1}2 = \ldots$$

If they touch also at the point P_1, we shall have also

$$10 : 1^{n-1}0 = 12 : 1^{n-1}2 = \ldots,$$

and so on for other points; so that when the surfaces touch at the point P_1, we shall have

$$\left.\begin{aligned}
\theta : 1^{n-1}0 &= 12 : 0^{n-1}1 \,.\, 1^{n-1}2,\\
\theta : 1^{n-1}0 &= 13 : 0^{n-1}1 \,.\, 1^{n-1}3,\\
\ldots \qquad &\qquad \ldots;
\end{aligned}\right\} \quad \ldots\ldots\ldots\ldots \quad (6)$$

when they touch also at the point P_2 we shall have

$$\left.\begin{aligned}
\theta : 2^{n-1}0 &= 21 : 0^{n-1}2 \,.\, 2^{n-1}1,\\
\theta : 2^{n-1}0 &= 23 : 0^{n-1}2 \,.\, 2^{n-1}3,\\
\ldots \qquad &\qquad \ldots,
\end{aligned}\right\} \quad \ldots\ldots\ldots\ldots \quad (7)$$

and so on for other points of contact.

These equations show that if the surfaces touch only at the point P, there is no means of eliminating any of the ratios $\theta : 12$, $\theta : 13$, .. If, however, they touch also at a second point P_1, we can eliminate all the ratios of the form $\theta : 12$; *i. e.* those containing the symbol 1 in the denominator. If the surfaces touch at a third point P_2, we can eliminate all the ratios of the form $\theta : 12$, $\theta : 13$, $\theta : 23$; viz. all those containing either of the symbols 1 or 2 in the denominator. It may be remarked that when the surfaces

touch at the three points P, P_1, P_2, the ratio $\theta : 12$ may be eliminated by either of the two formulæ

$$\left.\begin{aligned} \theta : 1^{n-1}0 &= 12 : 0^{n-1}1 \,.\, 1^{n-1}2, \\ \theta : 2^{n-1}0 &= 21 : 0^{n-1}2 \,.\, 2^{n-1}1. \end{aligned}\right\} \quad \ldots\ldots\ldots \quad (8)$$

That the conditions so obtained are equivalent to one another, and not independent, is both obvious *à priori* and is capable of being shown by multiplying the denominators of the first of the equations by $2^{n-1}0$ and those of the second by $1^{n-1}0$. The equations then take the form

$$\begin{aligned} \theta : 1^{n-1}0 \,.\, 2^{n-1}0 &= 12 : 0^{n-1}1 \,.\, 1^{n-1}2 \,.\, 2^{n-1}0 \\ &= 21 : 0^{n-1}2 \,.\, 2^{n-1}1 \,.\, 1^{n-1}0. \end{aligned}$$

But since the surfaces touch at the three points P, P_1, P_2, the last two denominators are in virtue of (18) of § 1 equal. Hence each one of the two equations (8) involves the other as a consequence.

Returning to the equations (5) and eliminating the ratios $\theta : 12, \ldots$, we obtain the three conditions:

$$\left.\begin{aligned} 1^{n-1}0A^2_{12}U + 0^{n-1}1 \,.\, 1^{n-1}2B_{12}U &= 0, \\ 1^{n-1}0A^2_{13}U + 0^{n-1}1 \,.\, 1^{n-1}3B_{13}U &= 0, \\ 1^{n-1}0A^2_{14}U + 0^{n-1}1 \,.\, 1^{n-1}4B_{14}U &= 0. \end{aligned}\right\} \quad \ldots\ldots\ldots \quad (9)$$

If the surfaces touch at a third point P_2, we may replace the equation $\square^2_{14}U=0$ by $\square^2_{23}U=0$. If they touch also at the point P_3, the results of elimination may be put into two forms, viz.

$$\left.\begin{aligned} &2^{n-1}0A^2_{23}U + 0^{n-1}2 \,.\, 2^{n-1}3B_{23}U = 0, \quad 3^{n-1}0A^2_{23}U + 0^{n-1}3 \,.\, 3^{n-1}2B_{23}U = 0, \\ &3^{n-1}0A^2_{31}U + 0^{n-1}3 \,.\, 3^{n-1}1B_{31}U = 0, \quad 1^{n-1}0A^2_{31}U + 0^{n-1}1 \,.\, 1^{n-1}3B_{31}U = 0, \\ &1^{n-1}0A^2_{12}U + 0^{n-1}1 \,.\, 1^{n-1}2B_{12}U = 0, \quad 2^{n-1}0A^2_{12}U + 0^{n-1}2 \,.\, 2^{n-1}1B_{12}U = 0. \end{aligned}\right\} \quad (10)$$

If the surfaces touch only at the three points P, P_1, P_2, we shall have only the first form of the first equation, the second of the second, and either form of the third.

If the surfaces have three-branch contact at a second point P_1, we may derive the conditions to be fulfilled, by a similar process, from the system

$$\square^2_{02}U_1 = 0, \quad \square^2_{03}U_1 = 0, \quad \square^2_{04}U_1 = 0,$$

and so on for any number of points.

For four-branch contact the number of equations is four, which may be written thus:

$$\left.\begin{aligned} \theta A^2_{12}U + 3(12)B_{12}A_{12}U &= 0, \\ \theta A^2_{13}U + 3(13)B_{13}A_{13}U &= 0, \\ \theta A^2_{14}U + 3(14)B_{14}A_{14}U &= 0, \\ \theta A^2_{15}U + 3(15)B_{15}A_{15}U &= 0; \end{aligned}\right\} \quad \ldots\ldots\ldots \quad (11)$$

and if the surfaces touch not only at the two points P, P_1, but also at a third point P_2, the last equation may be replaced by

$$\theta A_{23}^2 U + 3(23)B_{23}A_{23}U = 0. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (12)$$

The results of the elimination of the ratios $\theta : 12, \ldots$ will be of the form

$$1^{n-1}0A_{12}^2 U + 3 \cdot 0^{n-1}1 \cdot 1^{n-1}2B_{12}A_{12}U = 0. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (13)$$

Similarly the five conditions for five-branch contact will be of the form

$$(1^{n-1}0)^3 A_{12}^4 U + 6 \cdot 1^{n-1}0 \cdot 0^{n-1}1 \cdot 1^{n-1}2B_{12}A_{12}^2 U + 3(0^{n-1}1 \cdot 1^{n-1}2)^2 (A^2 + B^2)U = 0, \quad (14)$$

and the six conditions for six-branch contact will be of the form

$$(1^{n-1}0)^3 A^3 U + 10 \cdot 1^{n-1}0 \cdot 0^{n-1}1 \cdot 1^{n-1}2BA^3 U + 5(0^{n-1}1 \cdot 1^{n-1}2)^2 B(A^2 + 3B^2)U = 0. \quad (15)$$

Recapitulating the results now obtained, we may form the subjoined Table for the possibility of contact of a quadric V with a given surface U, viz. simple contact at a point P_1, &c.

For contact at the point P.	Number of conditions.	Degrees of conditions in		
		Coefficients of U.	Coordinates of P.	Coordinates of P_1; of P_2, ..
3 branch . .	3	4	$3n-3$	$n+1$; 2
4 do. . .	4	5	$4n-5$	$n+2$; 3
5 do. . .	5	7	$5n-6$	$2n+2$; 4
6 do. . .	6	8	$6n-8$	$2n+4$; 5

To these of course must be added the conditions that P and P_1 lie on the surface U, viz. $U=0$, $U_1=0$, and that U and V touch at P.

If the surfaces have simple contact at a third point P_2, we must add the condition $U_2=0$, and the condition (18) of § 1; and similarly for every additional point at which they have simple contact.

If the surfaces have 3, 4, .. pointic contact at a second, third, .. point we must double, triple, .. the number of conditions for each such degree of contact; the degrees of the conditions remaining unchanged.

Suppose, then, that the quadric V touches the surface U in two points, P, P_1; then in order that the contact may become three-pointic at either of these points (say P), three conditions are necessary. And if $a, b, \ldots$ be the coefficients of U, these conditions may be expressed thus:

$$(a, b, \ldots)^4 (x, y, \ldots)^{2n-3} (x_1, y_1, \ldots)^{n+1} (x_2, y_2, \ldots)^2 = 0,$$
$$(a, b, \ldots)^4 (x, y, \ldots)^{2n-3} (x_1, y_1, \ldots)^{n+1} (x_3, y_3, \ldots)^2 = 0,$$
$$(a, b, \ldots)^4 (x, y, \ldots)^{2n-3} (x_1, y_1, \ldots)^{n+1} (x_4, y_4, \ldots)^2 = 0;$$

and if by means of these equations, together with the equation $U_1=0$, we eliminate the

coordinates of P_1, we shall have an equation in $x, y, ..$ which will determine a curve upon U at every point of which (P_1 being taken arbitrarily) it is possible to draw a quadric having three-pointed contact. The degree of the curve would appear to be $3(n-1)\,3n(n+1)^3 = 2n(n+1)(n^3-1)$.

But regarding the conditions in question as relations between the coefficients of U, we have three equations of the degree 4 and one of the degree 1. Hence we may conclude that through any two points in space we may describe 64 surfaces, whose equations contain 5 independent constants (*e. g.* quartic scrolls having twisted cubics for their nodal lines), such that a quadric may be drawn touching them in two points each, and having three-pointic contact at one of the two points.

This theorem admits of obvious generalizations; but, having reference to the provisional nature of the numerical results, it seems hardly worth while to make a statement of the theorems which will probably require qualification hereafter.

There is yet another way in which the equations of condition may be regarded. The conditions for three-pointic contact involve the coordinates of four points, P, P_1, P_2, P_3; *i. e.* twelve disposable quantities. These may be determined so as to satisfy twelve equations. Hence it appears that on a given surface we may take four points (4 equations), such that a quadric may be drawn touching the surface at the four points (2 equations), and having three-pointic contact at two of them (6 equations); *i. e.* $4+2+6=12$ equations in all.

Again, the conditions for four-pointic contact involve the coordinates of five points, $P, P_1, .. P_4$; *i. e.* fifteen disposable quantities. Hence we may conclude that on a given surface we may take five points (5 equations), such that a quadric may be drawn, and having three-pointic contact at three of them ($1+3\times 3=10$ equations); *i. e.* $5+10=15$ equations in all.

Or, again, on a given surface we may take five points (5 equations), such that a quadric may be drawn touching the surface in the five points (3 equations), and having four-pointic contact at one of them (3+4 equations); *i. e.* $5+3+3+4=15$ equations in all.

To these theorems others might doubtless be added.

§ 4. *On Points of Four-, Five-, Six-pointic Contact with a Quadric Surface.*

If, setting aside for the moment the question of multiple contact, we fix our attention upon a single point P, the formulæ established in the preceding section suggest certain conditions necessary for the existence on a surface of points of four-, five-, six-branch contact with a quadric. These may be described as the conditions for a quartitactic, quintactic, sextactic point on a surface. Now, referring to the equations (4), (6), and (7) of § 3, and to the process there used for the elimination of the quantities relating to the quadric V (*i. e.* 6, 12, 13, ..), it appears that, when the contact subsists for a single point only, we have available for the purposes of elimination the relations

$$\theta = 01 : 0^{n-1}1 = 02 : 0^{n-1}2 = \ldots,$$

but not the relations

$$\theta_1 = 10 : 1^{n-1}0 = 12 : 1^{n-1}2 = \dots$$

Consequently we cannot eliminate, in the manner there effected, the quantities relating to the quadric V from any of the six equations derived from the forms $U=0$, $\square U=0$, $\square^2 U=0$. We may, in fact, by means of these equations, determine six out of the nine constants of V, but that is all.

When, however, P is a quartitactic point, we have the four additional equations, say

$$\square^2_{23} U=0,\ \square^2_{31} U=0,\ \square^2_{12} U=0,\ \square^2_{14} U=0,$$

ten in all. From one, or two, or three of these we may, by means of the equations

$$\square^1_{23} U=0,\ \square^1_{31} U=0,\ \square^1_{12} U=0,$$

eliminate one, or two, or three of the quantities $\theta : 23$, $\theta : 31$, $\theta : 12$, and obtain conditions of the form

$$3A^2U \,.\, BAU - A^3U \,.\, BU = 0,$$

to which the proper suffixes 23, 31, 12 are to be appended.

By this means we may either determine all nine of the coefficients of the quadric, and have one condition of the above form; or we may determine eight of the coefficients, and have two such conditions; or, lastly, we may determine seven of the coefficients, and have three such conditions.

From this it would appear that, if we regard the conditions as equations in the coordinates of the point P, there will be a curve on U every point of which will be quartactic, with a single quadric at each point. Again, there will be a definite number of points which will be also quartactic, having a singly infinite number of quadrics having four-branch contacts at the points.

When P is a quintactic point, we have the five additional equations,

$$\square^4_{23} U=0,\ \square^4_{31} U=0,\ \square^4_{12} U=0,\ \square^4_{14} U=0,\ \square^4_{24} U=0.$$

From three, or four, of these we may eliminate three, or four, of the quantities $\theta : 23$, $\theta : 31$, $\theta : 12$, $\theta : 14$, by means of the equations

$$\square^3_{23} U=0,\ \square^3_{31} U=0,\ \square^3_{12} U=0,\ \square^3_{14} U=0,$$

and obtain results of the forms

$$(BU)^2 A^4 U - 6BU \,.\, A^2U \,.\, BAU + 3(A^2U)^2 (A^2 + B^2) U = 0,$$
$$3(BAU)^2 A^4 U - 6BAU \,.\, A^2U \,.\, BA^2U + (A^2U)^2 (A^2 + B^2) U = 0.$$

If we have previously determined the nine coefficients, or if we have determined eight only, and use one of the new equations for determining the ninth, or if we have determined only seven, and use two of the new equations for determining the two remaining coefficients, we shall have six conditions; or, lastly, if having determined seven only, we now determine one more, we shall have seven conditions.

When P is a sextactic point, we have the six additional equations,

$$\square^1_{23}U=0,\ \square^1_{31}U=0,\ \square^1_{12}U=0,\ \square^1_{14}U=0,\ \square^1_{24}U=0,\ \square^1_{34}U=0.$$

From four, or five, of these we may eliminate four, or five, of the quantities $\theta:23$, $\theta:31$, $\theta:12$, $\theta:14$, $\theta:24$, $\theta:34$, by means of the equations

$$\square^2_{23}U=0,\ \square^2_{31}U=0,\ \square^2_{12}U=0,\ \square^2_{14}U=0,\ \square^2_{24}U=0,$$

and obtain results of the forms

$$(BU)^2A^2U-10BU\,.\,A^2U\,.\,BA^2U+5(A^2U)^2(A^2+3B^2)U=0,$$

$$(BAU)^2A^2U-10BAU\,.\,A^2U\,.\,BA^2U+5(A^2U)^2(A^2+3B^2)U=0,$$

$$\begin{vmatrix} A^4U, & 6BA^2U, & 3(A^2+B^2)U, & . & \\ . & A^4U, & 6BA^2U, & 3(A^2+B^2)U & \\ A^3U, & 10BA^2U, & 5B(A^2+3B^2)U, & . & \\ . & A^3U, & 10BA^2U, & 5B(A^2+3B^2)U & \end{vmatrix}=0.$$

If either we have determined all the coefficients of the quadric, or if having determined only eight we use one of the last equations for determining the results, we shall have twelve conditions.

Recapitulating, the following is a Table of the number of conditions so found, and of their degrees in the several quantities contained in them:—

For a	No. of constants determined.	No. of conditions.	Degree of condition in the		
			Coordinates of P.	Coordinates of P_1, . .	Coefficients of U.
Quartitactic point . .	7	3	$2(3n-4)$	4	6
	8	2			
	9	1			
Quintactic point . .	7	$3+5 = 8$	$3(3n-4)$	6	9
	8	$2+5=3+4 = 7$	$11n-16$	5	11
	9	$1+5=2+4=3+3= 6$			
Sextactic point . .	7	$8+6 =14$	$2(5n-7)$	7	10
	8	$7+6=8+5 =13$	$6(2n-3)$	9	12
	9	$6+6=7+5=8+4=12$	$2(9n-14)$	11	18

§ 5. *On Multiple Contact of Cubics with other Surfaces.*

Hitherto we have considered in detail only the case of quadrics, that is to say, the conditions which must be fulfilled by the coefficients of a surface U in order that it may be possible to draw a quadric having contact of given orders with U at more than one point. There is of course a corresponding problem with cubics, and indeed with surfaces of any degree; but the question soon becomes so complicated that it may be doubted

whether the results would be worth having even if means were found for pushing the investigation much further. There is, however, one case, namely the osculation of cubics, in which it is possible within a moderate compass to arrive at a solution.

Thus, when V is a cubic,

$$\left.\begin{aligned} \square_{13}U &= 0^2 2\,.\,0^{n-1}1 - 0^2 1\,.\,0^{n-1}2, \\ \square^2_{13}U &= (0^2 2)^2 0^{n-2}1^2 - 2\,.\,0^2 2\,.\,0^2 1\,.\,0^{n-3}12 + (0^2 1)^2 0^{n-2}2^2 \\ &\quad - 0^2 1\,.\,02^2\,.\,0^{n-1}1 + (0^2 2\,.\,0^{n-1}1 + 0^2 1\,.\,0^{n-1}2)012 - 0^2 2\,.\,01^2\,.\,0^{n-1}2. \end{aligned}\right\} \quad . \quad . \quad (1)$$

But in the same way, as in the case of quadrics (22), we may put

$$\left.\begin{aligned} 0^2 1 &= \theta\, 0^{n-1}1, \quad 0^2 2 = \theta\, 0^{n-1}2, \\ 1^2 0 &= \theta_1 1^{n-1}0, \quad 2^2 0 = \theta_2 2^{n-1}0; \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (2)$$

and the conditions for osculation at the point P, viz. $\square^2_{12}U=0$, $\square^2_{21}U=0$, $\square^2_{13}U=0$, will then become

$$\left.\begin{aligned} 2\,.\,0^{n-2}\,.\,0^{n-3}\,.\,023 &= -\theta[0', 2, 3] \quad . \quad + \theta_2 2^{n-1}0(0^{n-3})^2 + \theta_3 3^{n-1}0(0^{n-2})^2, \\ 2\,.\,0^{n-3}\,.\,0^{n-1}\,.\,031 &= -\theta[0', 3, 1] + \theta_1 1^{n-1}0(0^{n-3})^2 + \quad . \quad + \theta_3 3^{n-1}0(0^{n-1})^2, \\ 2\,.\,0^{n-1}\,.\,0^{n-2}\,.\,012 &= -\theta[0', 1, 2] + \theta_1 1^{n-1}0(0^{n-2})^2 + \theta_2 2^{n-1}0(0^{n-1})^2 + \quad . \end{aligned}\right\} (3)$$

Similarly for osculation at a second point P, we should have

$$\left.\begin{aligned} 2\,.\,1^{n-3}\,.\,1^{n-1}0\,.\,130 &= \theta 0^{n-1}(1^{n-3})^2 - \theta_1[1', 3, 0] \quad . \quad + \theta_3 3^{n-1}1(1^{n-1}0)^2, \\ 2\,.\,1^{n-1}0\,.\,1^{n-2}\,.\,102 &= \theta 0^{n-1}1(1^{n-2})^2 - \theta_1[1', 0, 2] + \theta_2 2^{n-1}1(1^{n-1}0)^2 \quad . \\ 2\,.\,1^{n-2}\,.\,1^{n-3}\,.\,123 &= \quad . \quad - \theta_1[1', 2, 3] + \theta_2 2_{n-1}1(1^{n-3})^2 + \theta_3 3^{n-1}1(1^{n-2})^2; \end{aligned}\right\} \quad (4)$$

and for osculation at a third point P_1, we should have

$$\left.\begin{aligned} 2\,.\,2^{n-1}0\,.\,2^{n-1}1\,.\,201 &= \theta 0^{n-2}2(2^{n-1}1)^2 + \theta_1 1^{n-2}(2^{n-1}0)^2 - \theta_2[2', 0, 1] \quad . \\ 2\,.\,2^{n-1}1\,.\,2^{n-3}\,.\,213 &= \quad . \quad + \theta_1 1^{n-2}(2^{n-3})^2 - \theta_2[2', 1, 3] + \theta_3 3^{n-2}(2^{n-1}1)^2, \\ 2\,.\,2^{n-3}\,.\,2^{n-1}0\,.\,230 &= \theta 0^{n-2}2(2^{n-3})^2 \quad . \quad - \theta_2[2', 3, 0] + \theta_3 3^{n-2}(2^{n-1}0)^2. \end{aligned}\right\} \quad (5)$$

These together form a system of nine equations involving the seven quantities $123 : 230 : 301 : 012 : \theta : \theta_1 : \theta_2 : \theta_3$. We can therefore eliminate these quantities in two different ways; in other words, there will be two relations between the coefficients of the equation of the surface U. In order to determine the degrees of these resultants in the coefficients in question, consider first the three equations in $012, \theta, \theta_1, \theta_2$. The degrees of the coefficients of these quantities (in the coefficients of U) are 2, 3, 3, 3 respectively; hence the quantities $\theta, \theta_1, \theta_2$ will be proportionate to expressions which are of the degrees $3+3+2=8$. Next taking the two equations involving 123, and eliminating that quantity between them, we shall obtain an equation in $\theta_1, \theta_2, \theta_3$, the coefficients of which are of the degree 5 in those of U. Similarly from the others we should obtain equations in $\theta, \theta_1, \theta_2$; $\theta, \theta_1, \theta_3$; whose coefficients are of the same degree.

From these equations we can, by means of the values of the ratios $\theta : \theta_1 : \theta_2$, eliminate θ, θ_1, θ_2, θ_3 in two different ways; and the resulting equations will be of the degree $5+5+8=18$.

Proceeding to perform the actual eliminations, and taking the three equations involving 012, we find that the ratios

$$-2\,.\,012 : -\theta : \theta_1 : -\theta_2$$

are proportional to the determinants of the matrix,

$$\begin{array}{llll} 0^{n-1}1\,.\,0^{n-1}2, & -[0', 1, 2], & 1^{n-1}0(0^{n-1}2)^2, & 2^{n-1}0(0^{n-1}1)^2, \\ 1^{n-1}2\,.\,1^{n-1}0, & 0^{n-1}1(1^{n-1}2)^2, & -[0, 1', 2], & 2^{n-1}1(1^{n-1}0)^2, \\ 2^{n-1}0\,.\,2^{n-1}1, & 0^{n-1}2(2^{n-1}1)^2, & 1^{n-1}2(2^{n-1}0)^2, & -[0, 1, 2']; \end{array}$$

viz. the quantity to which θ is proportional will be

$$\begin{aligned} & 0^{n-1}1[0, 1', 2]0^{n-1}2[0, 1, 2'] \\ & +0^{n-1}1[0, 1', 2](2^{n-1}0)^2 2^{n-1}1\,.\,0^{n-1}1 \\ & +0^{n-1}2[0, 1, 2'](1^{n-1}0)^2 0^{n-1}2\,.\,1^{n-1}2 \\ & -0^{n-1}1\,.\,0^{n-1}2\,.\,(1^{n-1}0)^2(2^{n-1}0)^2 1^{n-1}2\,.\,2^{n-1}1 \\ & +1^{n-1}0(0^{n-1}1)^2(1^{n-1}2)^2(2^{n-1}0)^2 2^{n-1}0 \\ & +2^{n-1}0(1^{n-1}0)^2(0^{n-1}2)^2(2^{n-1}1)^2 1^{n-1}0\,; \end{aligned}$$

and writing, for brevity,

$$\left.\begin{aligned} & 2^{n-1}3\,.\,3^{n-1}1\,.\,1^{n-1}2 - 3^{n-1}2\,.\,1^{n-1}3\,.\,2^{n-1}1 = P_{123}, \\ & 2^{n-1}3\,.\,3^{n-1}0\,.\,0^{n-1}2 - 3^{n-1}2\,.\,0^{n-1}3\,.\,2^{n-1}0 = P_{023}, \\ & 1^{n-1}3\,.\,3^{n-1}0\,.\,0^{n-1}1 - 3^{n-1}1\,.\,0^{n-1}3\,.\,1^{n-1}0 = P_{013}, \\ & 1^{n-1}2\,.\,2^{n-1}0\,.\,0^{n-1}1 - 2^{n-1}1\,.\,0^{n-1}2\,.\,1^{n-1}0 = P_{012}, \end{aligned}\right\} \quad \ldots\ldots \quad (6)$$

and forming expressions symmetrical to that written above, we shall find that they may all be put into the following shape:—

$$\begin{aligned} & \theta : \theta_1 : \theta_2 \\ & = \big([0, 1', 2]0^{n-1}1 + (1^{n-1}0)^2 0^{n-1}2\,.\,1^{n-1}2\big)\big([0, 1, 2']0^{n-1}2 + (2^{n-1}0)^2 0^{n-1}1\,.\,2^{n-1}1\big) \\ & \qquad + 1^{n-1}0\,.\,2^{n-1}0 P_{012}^2 \\ & : \big([0, 1, 2']1^{n-1}2 + (2^{n-1}1)^2 1^{n-1}0\,.\,2^{n-1}0\big)\big([0', 1, 2]1^{n-1}0 + (0^{n-1}1)^2 0^{n-1}2\,.\,1^{n-1}2\big) \\ & \qquad + 2^{n-1}1\,.\,0^{n-1}1 P_{012}^2 \\ & : \big([0', 1, 2]2^{n-1}0 + (0^{n-1}2)^2 2^{n-1}1\,.\,0^{n-1}1\big)\big([0, 1', 2]2^{n-1}1 + (1^{n-1}2)^2 1^{n-1}0\,.\,2^{n-1}0\big) \\ & \qquad + 0^{n-1}2\,.\,1^{n-1}2 P_{012}^2 \end{aligned} \quad \left.\begin{array}{l} \\ \\ \\ \\ \\ \\ \\ \end{array}\right\} \quad (7)$$

Again, from the two equations involving 123, we obtain by elimination

$$\left.\begin{aligned} & -\big([1', 2, 3]2^{n-1} + (1^{n-1}2)^2 1^{n-1}3\,.\,2^{n-1}3\big)2^{n-1}3\theta_1 \\ & +\big([1, 2', 3]1^{n-1}2 + (2^{n-1}1)^2 1^{n-1}3\,.\,2^{n-1}3\big)1^{n-1}3\theta_2 + 1^{n-1}2\,.\,2^{n-1}1 P_{123}\theta_3 = 0. \end{aligned}\right\} \quad . \quad (8)$$

Similarly from the two equations in 023 we obtain

$$\left.\begin{aligned} &-\big([0', 2, 3]2^{n-1}0+(0^{n-1}2)^{n}2^{n-1}3\,.\,0^{n-1}3\big)2^{n-1}3\theta \\ &+\big([0, 2', 3]0^{n-1}2+(2^{n-1}0)^{n}2^{n-1}3\,.\,0^{n-1}3\big)0^{n-1}3\theta_2+0^{n-1}2\,.\,2^{n-1}0\mathrm{P}_{023}\theta_3=0; \end{aligned}\right\} \quad . \quad (9)$$

and from the two equations in 013

$$\left.\begin{aligned} &-\big([0', 1, 3]1^{n-1}0+(0^{n-1}1)^{n}0^{n-1}3\,.\,1^{n-1}3\big)1^{n-1}3\theta \\ &+\big([0, 1', 3]0^{n-1}1+(1^{n-1}0)^{n}0^{n-1}3\,.\,1^{n-1}3\big)0^{n-1}3\theta_1+0^{n-1}1\,.\,1^{n-1}0\mathrm{P}_{013}\theta=0. \end{aligned}\right\} \quad . \quad (10)$$

If we now put

$$\left.\begin{aligned} &[1, 2', 3]1^{n-1}2+(2^{n-1}1)^{n}2^{n-1}3\,.\,1^{n-1}3=\mathrm{B}, \\ &[1, 2, 3']1^{n-1}3+(3^{n-1}1)^{n}3^{n-1}2\,.\,1^{n-1}2=\mathrm{B}', \\ &[1, 2, 3']2^{n-1}3+(3^{n-1}2)^{n}3^{n-1}1\,.\,2^{n-1}1=\mathrm{C}, \\ &[1', 2, 3]2^{n-1}1+(1^{n-1}2)^{n}1^{n-1}3\,.\,2^{n-1}3=\mathrm{C}', \\ &[1', 2, 3]3^{n-1}1+(1^{n-1}3)^{n}1^{n-1}2\,.\,3^{n-1}2=\mathrm{D}, \\ &[1, 2', 3]3^{n-1}2+(2^{n-1}3)^{n}2^{n-1}1\,.\,3^{n-1}1=\mathrm{D}', \\ &[2', 3, 0]0^{n-1}2+(2^{n-1}0)^{n}2^{n-1}3\,.\,0^{n-1}3=\mathrm{F}, \\ &[2, 3', 0]0^{n-1}3+(3^{n-1}0)^{n}3^{n-1}2\,.\,0^{n-1}2=\mathrm{F}', \\ &[2, 3', 0]2^{n-1}3+(3^{n-1}2)^{n}3^{n-1}0\,.\,2^{n-1}0=\mathrm{H}, \\ &[2, 3, 0']2^{n-1}0+(0^{n-1}2)^{n}0^{n-1}3\,.\,2^{n-1}3=\mathrm{H}', \\ &[2, 3, 0']3^{n-1}0+(0^{n-1}3)^{n}0^{n-1}2\,.\,3^{n-1}2=\mathrm{K}, \\ &[2', 3, 0]3^{n-1}2+(2^{n-1}3)^{n}2^{n-1}0\,.\,3^{n-1}0=\mathrm{K}', \\ &[3, 0, 1']0^{n-1}1+(1^{n-1}0)^{n}1^{n-1}3\,.\,0^{n-1}3=\mathrm{L}, \\ &[3', 0, 1]0^{n-1}3+(3^{n-1}0)^{n}3^{n-1}1\,.\,0^{n-1}1=\mathrm{L}', \\ &[3', 0, 1]1^{n-1}3+(3^{n-1}1)^{n}3^{n-1}0\,.\,1^{n-1}0=\mathrm{M}, \\ &[3, 0', 1]1^{n-1}0+(0^{n-1}1)^{n}0^{n-1}3\,.\,1^{n-1}3=\mathrm{M}', \\ &[3, 0', 1]3^{n-1}0+(0^{n-1}3)^{n}0^{n-1}1\,.\,3^{n-1}1=\mathrm{O}, \\ &[3, 0, 1']3^{n-1}1+(1^{n-1}3)^{n}1^{n-1}0\,.\,3^{n-1}0=\mathrm{O}', \\ &[0, 1', 2]0^{n-1}1+(1^{n-1}0)^{n}1^{n-1}2\,.\,0^{n-1}2=\mathrm{P}, \\ &[0, 1, 2']0^{n-1}2+(2^{n-1}0)^{n}2^{n-1}1\,.\,0^{n-1}1=\mathrm{P}', \\ &[0, 1, 2']1^{n-1}2+(2^{n-1}1)^{n}2^{n-1}0\,.\,1^{n-1}0=\mathrm{Q}, \\ &[0', 1, 2]1^{n-1}0+(0^{n-1}1)^{n}0^{n-1}2\,.\,1^{n-1}2=\mathrm{Q}', \\ &[0', 1, 2]2^{n-1}0+(0^{n-1}2)^{n}0^{n-1}1\,.\,2^{n-1}1=\mathrm{R}, \\ &[0, 1', 2]2^{n-1}1+(1^{n-1}2)^{n}1^{n-1}0\,.\,2^{n-1}0=\mathrm{R}'. \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad (11)$$

Substituting these values in the equations (7) . . (10) for determining θ, θ_1, θ_2, θ_3, we shall obtain the following expressions:—

For osculation at the points P_1, P_2, P_3,

$$\left.\begin{aligned}
\theta_1 : \theta_2 : \theta_3 = {} & BB' + 2^{n-1}1 \,.\, 3^{n-1}1P^2_{123} \\
: {} & CC' + 3^{n-1}2 \,.\, 1^{n-1}2P^2_{123} \\
: {} & DD' + 1^{n-1}3 \,.\, 2^{n-1}3P^2_{123}, \\
K'3^{n-1}0\theta_2 - H2^{n-1}0\theta_3 - 2^{n-1}3 \,.\, 3^{n-1}2P_{023}\theta = 0, \\
M'1^{n-1}0\theta_3 - O'3^{n-1}0\theta_1 - 3^{n-1}1 \,.\, 1^{n-1}3P_{013}\theta = 0, \\
R'2^{n-1}0\theta_1 - Q\,1^{n-1}0\theta_2 - 1^{n-1}2 \,.\, 2^{n-1}1P_{012}\theta = 0.
\end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad (12)$$

Similarly for osculation at the points P, P_2, P_3,

$$\left.\begin{aligned}
\theta : \theta_2 : \theta_3 = {} & FF' + 2^{n-1}0 \,.\, 3^{n-1}0P^2_{023} \\
: {} & HH' + 3^{n-1}2 \,.\, 0^{n-1}2P^2_{023} \\
: {} & KK' + 0^{n-1}3 \,.\, 2^{n-1}3P^2_{023}, \\
D'3^{n-1}1\theta_2 - C\,2^{n-1}1\theta_3 - 2^{n-1}3 \,.\, 3^{n-1}2P_{123}\theta_1 = 0, \\
L'0^{n-1}1\theta_3 - O\,3^{n-1}1\theta - 3^{n-1}0 \,.\, 0^{n-1}3P_{013}\theta_1 = 0, \\
R\,2^{n-1}1\theta - P'0^{n-1}1\theta_3 - 0^{n-1}2 \,.\, 2^{n-1}0P_{013}\theta_1 = 0.
\end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad (13)$$

Similarly for osculation at the points P, P_1, P_3,

$$\left.\begin{aligned}
\theta : \theta_1 : \theta_3 = {} & LL' + 1^{n-1}0 \,.\, 3^{n-1}0P^2_{013} \\
: {} & MM' + 3^{n-1}1 \,.\, 0^{n-1}1P^2_{013} \\
: {} & OO' + 0^{n-1}3 \,.\, 1^{n-1}3P^2_{013}, \\
D3^{n-1}2\theta_1 - B'\,1^{n-1}2\theta_3 - 1^{n-1}3 \,.\, 3^{n-1}1P_{123}\theta_2 = 0, \\
F'0^{n-1}2\theta_3 - K\,3^{n-1}2\theta - 3^{n-1}0 \,.\, 0^{n-1}3P_{023}\theta_2 = 0, \\
Q'1^{n-1}2\theta - P\,0^{n-1}2\theta_1 - 0^{n-1}1 \,.\, 1^{n-1}0P_{012}\theta_2 = 0.
\end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad (14)$$

And for osculation at the points P, P_1, P_2,

$$\left.\begin{aligned}
\theta : \theta_1 : \theta_2 = {} & PP' + 1^{n-1}0 \,.\, 2^{n-1}0P^2_{012} \\
: {} & QQ' + 2^{n-1}1 \,.\, 0^{n-1}1P^2_{012} \\
: {} & RR' + 0^{n-1}2 \,.\, 1^{n-1}2P^2_{012}, \\
C'2^{n-1}3\theta_1 - B\,1^{n-1}3\theta_2 - 1^{n-1}2 \,.\, 2^{n-1}1P_{123}\theta_3 = 0, \\
F\,0^{n-1}3\theta_2 - H'2^{n-1}3\theta - 2^{n-1}0 \,.\, 0^{n-1}2P_{023}\theta_3 = 0, \\
M'1^{n-1}3\theta - L\,0^{n-1}3\theta_1 - 0^{n-1}1 \,.\, 1^{n-1}0P_{013}\theta_3 = 0.
\end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad (15)$$

Whence, finally, the two conditions for osculation at the points P_1, P_2, P_3, together with simple contact at the four points P, P_1, P_2, P_3, will be

$$\left.\begin{aligned}
& \{K'(CC' + 3^{n-1}2 \,.\, 1^{n-1}2P^2_{123})3^{n-1}0 - H(DD' + 1^{n-1}3 \,.\, 2^{n-1}3P^2_{123})2^{n-1}0\} : 2^{n-1}3 \,.\, 3^{n-1}2P_{023} \\
= {} & \{M(DD' + 1^{n-1}3 \,.\, 2^{n-1}3P^2_{123})1^{n-1}0 - O'(BB' + 2^{n-1}1 \,.\, 3^{n-1}1P^2_{123})3^{n-1}0\} : 3^{n-1}1 \,.\, 1^{n-1}3P_{013} \\
= {} & \{B'(BB' + 2^{n-1}1 \,.\, 3^{n-1}1P^2_{123})2^{n-1}0 - Q(CC' + 3^{n-1}2 \,.\, 1^{n-1}2P^2_{123})1^{n-1}0\} : 1^{n-1}2 \,.\, 2^{n-1}1P_{012},
\end{aligned}\right\} \quad (16)$$

and similarly for the other groups of points. The degree of these equations, when cleared of fractions, is obviously 18, as stated above.

The requisite conditions are consequently, four of the form $1^{\alpha}=0$, $2^{\alpha}=0$, . . , of the degrees 1, 1, 1, 1, in the coefficients of U; and two of the degree 18 in the same quantities; six in all. And from these data theorems corresponding to those enunciated for contact by a quadric may be written down.

It is, however, to be noticed that if osculation subsist at four points P, P_1, P_2, P_3, then we have simultaneously the equations

$$\left.\begin{array}{llll} \theta_1 : \theta_2 : \theta_3 = . & : BB' + . . & : CC' + . . & : DD' + . . , \\ \theta : . : \theta_2 : \theta_3 = FF' + . . & : . & : HH' + . . & : KK' + . . , \\ \theta : \theta_1 : . : \theta_3 = LL' + . . & : MM' + . . & : . & : OO' + . . , \\ \theta : \theta_1 : \theta_2 : . = PP' + . . & : QQ' + . . & : RR' + . . & : . \end{array}\right\} \quad . \quad . \quad . \quad . \quad (17)$$

any two rows of which being taken as independent the remaining two are consequences. Taking any two we can eliminate one of the ratios $\theta : \theta_1 : \theta_2 : \theta_3$, and thus obtain as one of the conditions an equation of the degree 16.

In this case, therefore, there will be four conditions of the degree 1, three of the degree 18, and one of the degree 16.

In certain special cases these expressions undergo considerable modification. Thus, if the surface U be capable of being touched by a quadric, as well as being osculated by a cubic in the four points P, P_1, P_2, P_3, we shall have, as proved above,

$$P_{123}=0, \quad P_{023}=0, \quad P_{013}=0, \quad P_{012}=0;$$

and the system of conditions for the osculation between the cubic V and the surface U will take the following form:—

$$\left.\begin{array}{l} \left.\begin{array}{l} K'CC'\ 3^{\alpha-1}0 - HDD'\ 2^{\alpha-1}0 = 0, \\ MDD'\ 1^{\alpha-1}0 - O'BB'\ 3^{\alpha-1}0 = 0, \\ R'BB'\ 2^{\alpha-1}0 - QCC'\ 1^{\alpha-1}0 = 0, \end{array}\right\} \\ \left.\begin{array}{l} D'HH'3^{\alpha-1}1 - CKK'\ 2^{\alpha-1}1 = 0, \\ L'KK'0^{\alpha-1}1 - OFF'\ 3^{\alpha-1}1 = 0, \\ RFF'\ 2^{\alpha-1}1 - P'HH'0^{\alpha-1}1 = 0, \end{array}\right\} \\ \left.\begin{array}{l} DMM'3^{\alpha-1}2 - B'OO'\ 1^{\alpha-1}2 = 0, \\ FOO'\ 0^{\alpha-1}2 - KLL'\ 3^{\alpha-1}2 = 0, \\ QLL'\ 1^{\alpha-1}2 - PMM'0^{\alpha-1}2 = 0, \end{array}\right\} \\ \left.\begin{array}{l} C'QQ'\ 2^{\alpha-1}3 - BRR'\ 1^{\alpha-1}3 = 0, \\ FRR'\ 0^{\alpha-1}3 - HPP'\ 2^{\alpha-1}3 = 0, \\ MPP'\ 1^{\alpha-1}3 - LQQ'\ 0^{\alpha-1}3 = 0, \end{array}\right\} \end{array}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (18)$$

of which four groups two only will of course be independent. It appears, therefore, that for osculation at three points we have three conditions, and for osculation at four points six, when the surface can be touched by a quadric at the four points, instead of two, or four, as in the case when such contact is not presupposed. The degree of these conditions is 13; but one of each three may be depressed to the degree 12 by multiplying together the dexter and sinister sides of these expressions and dividing out the common factor $BB'CC'DD'1^{n-1}0 \,.\, 2^{n-1}0 \,.\, 3^{n-1}0$, &c. The results, by the help of the relations (17), may in the case of osculation at the four points be put into either of the following forms, viz.:—

$$\left.\begin{aligned} K'MR' &= HO'Q, & KM'R &= H'OQ', \\ D'L'R &= COP', & DLR' &= C'O'P, \\ DF'Q' &= B'KP, & D'FQ &= BK'P', \\ C'FM &= BH'L, & CF'M &= B'HL'. \end{aligned}\right\} \quad \ldots\ldots\ldots \quad (19)$$

The arrangement of the letters in these equations will be perhaps more readily apprehended by reference to the matrix written below; by which it appears that the combinations, accents apart, follows that of the principal minors of the determinant,

$$\begin{matrix} ., & B, & C, & D, \\ F, & . & H, & K, \\ L, & M, & . & O, \\ P, & Q, & R, & . \end{matrix}$$

The total conditions will in this case be, four of the degree 1, four of the degree 13, and two of the degree 12.

The form of the above equations will perhaps be best seen by actually writing down the first, viz.

$$\begin{vmatrix} . & [01'2]2^{n-1}1+.. & [01'3]3^{n-1}1+.. \\ [02'1]1^{n-1}2+.. & . & [02'3]3^{n-1}2+.. \\ [03'1]1^{n-1}3+.. & [03'2]2^{n-1}3+.. & . \end{vmatrix} = 0. \quad \ldots \quad (20)$$

X. *On the Development of the Teeth of Fishes* (Elasmobranchii *and* Teleostei).

By Charles S. Tomes, *M.A.* *Communicated by* John Tomes, *F.R.S.*

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The conformation of the jaws of the Elasmobranchii is such as to afford peculiar facilities for the study of the development of their teeth, and it has hence resulted that the older descriptions of the process approximate more closely to the truth than has been found to be the case in reptiles and mammals, and, I may now add, in osseous fish.

The accounts given by Prof. Owen in his 'Odontography' (p. 35) and 'Anatomy of Vertebrates' (vol. i. p. 381) do not materially differ from one another; I will therefore make an extract from the latter work as embodying as concisely as possible the views of that anatomist, which are generally accepted as correct:—

"It is interesting to observe in it (the class of Fishes) the process arrested at each of the well-marked stages through which the development of a mammalian tooth passes. In all fishes the first step is the simple production of a soft vascular papilla from the free surface of the buccal membrane; in sharks and rays these papillæ do not proceed to sink into the substance of the gum, but are covered by caps of an opposite free fold of the buccal membrane; these caps do not contract any organic connexion with the papilliform matrix, but, as this is converted into dental tissue, the tooth is gradually withdrawn from the extraneous protecting-caps, to take its place and assume the erect position on the margin of the jaw.

"Here, therefore, is represented the first and transitory 'papillary' stage of dental development in mammals, and the simple crescentic cartilaginous maxillary plate, with the open groove behind, containing the germinal papillæ of the teeth, offers in the shark a magnified representation of the earliest condition of the jaws and teeth in the human embryo."

My own observations do not enable me to verify in its entirety any portion of the above extract, some of the conclusions expressed in which had, indeed, already been challenged by Professor Huxley* in a paper published in the 'Quarterly Journal of Microscopical Science' in 1853.

* In the first part of the Philosophical Transactions for 1875 I have already given a brief *résumé* of the present state of knowledge on the subject of the development of teeth; and I have therefore incorporated in the text of the present paper references to those papers only which directly relate to the teeth of Fish. As, however, this paper will not appear in the same volume of the Transactions, I very gladly fall in with the suggestion that I should notice one or two salient points lately established as true of other teeth.

Prof. Huxley (Quart. Journ. Micros. Sci. 1853), while accepting the views of Goodsir as true of mammalian teeth, combated the idea that all reptilian and piscine teeth were developed from free papillæ; Guillot (Annal.

To confine the discussion for the present to the Elasmobranch Fishes, Professor Owen, as shown in the above quotation, holds that their teeth stop short at a "papillary" stage equivalent to that supposed by him to exist at an early stage of the formation of a human tooth; while against this we have the opinion of Professor Huxley, that "the process seems to correspond with something more than the first and transitory papillary stage of the development of the mammalian teeth."

The application of modern methods of microscopic research has rendered it possible to obtain sections showing the relation of the various structures over a far larger area than was formerly practicable; and the facts thus brought to light appear to me to be of sufficient interest to merit careful description, although in many of the essential points I have been anticipated by Professor Huxley, as is shown by the extract here subjoined.

"In the Skate, as is well known, the young teeth are developed in longitudinal rows within a deep fold of the mucous membrane of the mouth, behind the jaw. So far as my examinations go, however, I find that this is not a mere simple fold, such as it has been described to be, but its two walls behave just in the same manner as those of the primitive dental groove in man—that is, they become closely united in lines perpendicular to the direction of the jaw, so that partitions are formed between every two rows of teeth; transverse partitions again stretch between the separate teeth of each row, but these did not appear to me to be complete, terminating by an arcuated border below. Each longitudinal canal, therefore, answers to a single elongated mammalian follicle, or to that prolongation of the alveolar groove from which the posterior permanent molars are formed in man (see Goodsir), only the process does not go so far as in this case, the separate capsules remaining imperfect anteriorly and posteriorly. The lateral walls of the capsule, however, seem to me to have as much (or as little) 'organic

d. Sci. Nat. 1850) gave figures of young mammalian tooth-germs, which were very nearly correct; but the more precise knowledge which we now possess of the sequence of events in the formation of a tooth-germ is due to Prof. Kölliker (Zeitschr. f. wiss. Zool. 1863, and Gewebelehre, 5th edition).

Kölliker demonstrates that an ingrowth of epithelium (termed by him "enamel-germ"), which was afterwards destined to become the enamel-organ, was first recognizable before the dentine-pulp became visible; and, further, that the enamel-germ of a permanent tooth was derived from a part of the enamel-organ of its deciduous predecessor, this constituting the sole genetic relation between the two tooth-germs. Lœnos and Magitot added (Journ. de l'Anat. et Phys. 1873) an account of the origin of the tooth-germs of the true molars. Of fish, Prof. Kölliker in his earlier work (Mikroskopische Anatomie, 1854, B. ii. p. 114) states, agreeing with Prof. Owen, that the teeth of Plagiostomes are developed from free papillæ, and that they have therefore no enamel, never having been enclosed in sacs. This last inference is not confirmed by my own observations, nor by those of Hertwig, quoted at a later page.

Prof. Kölliker goes on to say that the teeth of all other fish (than Plagiostomes) are developed in sacs, sometimes enclosed within the jaw, sometimes only in mucous membrane, the successional teeth being developed anew from the mucous membrane of the mouth, behind the older teeth. The presence of an enamel-organ he considers to depend upon the existence of an enamel-like layer upon the teeth; in this last respect I have arrived at a different conclusion, being convinced that an enamel-organ is of universal occurrence, although the degree of its after development does in a great measure depend upon the amount (if any) of enamel to be formed.

connexion with the pulp and attachment to its base' as in man; and the process seems to correspond with something more than the 'first and transitory papillary stage of the development of the mammalian teeth.'

"Each pulp is invested by a very distinct basement membrane, whose continuity with that of the mucous membrane of the follicle is very obvious. The epithelium of the follicle forms a thick layer, which sometimes, when the upper wall is stripped back, adheres to it—sometimes remains as a cap investing the papilla. Even when the latter does not take place shreds of the epithelium frequently adhere to the papilla in the form of irregular, more or less cylindrical nucleated cells; as often, however, the papilla, whether any of the proper tooth substances be formed or not, has nothing adherent to it, but presents a perfectly smooth sharp edge."—"On the Development of the Teeth," Quart. Journ. Microsc. Science, 1853, p. 151.

Any fortunate transverse section through the jaws of a rather young dogfish affords an excellent view of the relation of the various parts to one another.

The dense gum or mucous membrane covering the convexity of the jaw is seen to be continuous with the softer and less fibrous tissue from which spring the dentine-papillæ near to the base of the jaw (Plate 31*. fig. 1), and this again is continuous with the connective-tissue framework of the protecting "thecal" fold. The sheet of tissue from which, at the base of the jaw, young dentine-papillæ originate becomes more fibrous as it passes upwards over the jaw, while those portions which intervene between the bases of the formative papillæ have their fibres specially arranged with reference to the teeth, so as to form in some sort ligaments to secure them in place (see fig. 2), running from the base of one tooth to that of the next.

The youngest dentine-papilla is a simple hemispherical eminence; that next in age is conical, while above this point the characteristic form of the future tooth is more closely approached.

In the youngest dentine-germs of the dogfish the cells near to the surface are larger than those more deeply situated, and measure about $\frac{1}{3000}$ of an inch in length; in older germs the larger size and greater abundance of the cells upon the surface is noteworthy, but nothing at all comparable to the distinct odontoblast layer or membrana eboris, characteristic of the formative organs of hard unvascular dentine, is met with.

It is not, however, so much in the dentine-papillæ as in their epithelium that the chief interest lies, especially when the facts described by myself in a former communication upon the development of the teeth in Batrachia and Reptilia† are kept in view for the sake of comparison.

Tracing the epithelium downwards from the exposed convex surface of the jaw (*a*, fig. 1) it is seen, opposite to the interspace between the third and fourth teeth, to leave the jaw and spring across to invest the thecal fold. In the specimen figured it has been

† As well as the sequence of events occurring in the formation of mammalian germs as demonstrated by Prof. Kölliker, *loc. cit.*

torn at this point, as often happens, and the continuity is therefore interrupted at *f* in the figure.

All that lies below this point is situated, therefore, not in an open groove, but in a closed space, roofed in and filled in by epithelium; the significance of this fact only becomes fully apparent when taken in conjunction with what is observed in other creatures.

Below this point the epithelium is continued down in the interspace between the jaw and the thecal fold, and forms investing caps to each of the dentine-papillæ—attaining, opposite to the youngest of the latter, a degree of development apparently in advance of and almost disproportionate to the stage of evolution of the papilla.

Their homologies, and the degree of development which they attain, entitle these epithelial caps to the name of "enamel-organs"*; and it was first pointed out by Professor Huxley, in the paper to which I have already referred, that enamel-organs are "nothing more than altered epithelium"†.

The structure of these enamel-organs is not very dissimilar to that of the corresponding organs in other Fish and Reptiles; their most conspicuous part is a layer of regular large columnar cells ("enamel-cells"), furnished with nuclei at their attached ends, and measuring from $\frac{1}{500}$ to $\frac{1}{100}$ of an inch in length. These "enamel-cells" are larger than, and different in appearance from, the cells to be met with elsewhere in the epithelium of the mouth; their occurrence, as well as the character of the residuum of the enamel-organ, justify us in saying that the epithelium "has in this situation undergone a special transformation into an 'enamel-organ.'"

Unless the specimen has been treated with acid the enamel-cells are often found to be firmly adherent to the cap of forming dentine; but after prolonged maceration in chromic acid they become detached, as is the case in the sections figured.

The extent to which enamel is formed upon the teeth of Elasmobranch Fishes is variable: it may seem an easy matter to pronounce whether there is or is not enamel upon any particular tooth; but in actual practice it is a matter of extreme difficulty to pronounce with any thing approaching to certainty upon the presence of an exceedingly thin layer of enamel upon the exterior of a tooth.

No one can doubt the existence of enamel upon the teeth of some skates; as the formative organs of the teeth of the skates are precisely similar, save in some details of form, to those of the dogfish, I do not doubt that the thin clear external layers upon the teeth of the latter are to be regarded as enamel.

The residual part of the enamel-organ is inconspicuous; it consists of very much smaller cells, branched and intercommunicating and forming a firmly fibrillated tissue; it is best seen in the youngest enamel-organ (fig. 2).

The enamel-organs of the successional teeth are so closely and intimately connected

* *Cf.* the "enamel-organs" of the dermal spines of dogfish, as described and figured by Hertwig, Jenaische Zeitschrift, 1874.

† Prof. Kölliker (Mikros. Anatomie, B. ii. p. 114) by inference denies the existence of an enamel-organ in the Plagiostomes; I am not aware of his having since altered his opinion.

that they may almost be termed a "compound enamel-organ;" and they thus recall the manner in which successive enamel-organs bud off from the necks of their predecessors in the newt.

The columnar cells (enamel-cells) remain upon the surface of the formed tooth until it has arrived at a point above the protection of the thecal fold (see the third tooth in fig. 1); after this they get worn off and lost.

In the interspaces of the teeth the "enamel-organs" lose their distinctive character, and between the older teeth do not markedly differ from the epithelium of other parts of the mouth.

In young dogfishes the partitions between the successional teeth, and also between the contiguous vertical rows, are formed solely by epithelium; but, as was pointed out by Professor Huxley, in older specimens septa of connective tissue separate each vertical row from those on either side of it, so that a tooth and its successors are contained in a sort of longitudinal canal, the whole series being connected together by the continuity of their enamel-organs.

In very young specimens, before any lip is formed, the transition of the dermal spines on the under surface of the head into the teeth is readily demonstrable.

Thus in fig. 3, which represents a section of the lower jaw of a very young dogfish, the spines upon the skin are seen to pass without breach of continuity into the teeth, from which they differ mainly in size, and to a very slight extent only in shape*.

It is stated by Gegenbaur (Manuel d'Anatomie Comparée, p. 738) that in *Selachia* the mucous membrane of the mouth, as far back as the pharynx, is clothed with spines of structure identical with that of the teeth proper, these spines often occupying those regions which in Ganoids and Teleostei are clothed with conspicuous teeth; I have not had the opportunity of myself verifying his statement†.

* Prof. Williamson (Phil. Trans. 1849) pointed out the structural resemblance of ganoid and placoid sides to teeth and their homological identity.

† To the above remarks must be added the statement of Hertwig (Jenaische Zeitschrift, 1874), that the teeth and the dermal spines are developed in a manner precisely similar. I did not become acquainted with his paper until after this paper had been read before the Royal Society, or I should have made more frequent reference to his results. Dr. Hertwig seems to have been working in the same groove as myself, and has published his paper relating to the development of the dermal spines and teeth of sharks a short time before mine was read; whilst a short time after my paper on the development of Batrachian teeth was read he published a contribution to the same subject. It is gratifying to find that the figures and descriptions of our independent and almost contemporaneous papers conform very closely, though there are points on which we differ.

Dr. Hertwig gives figures of dermal spines in the process of development in which a papilliform eminence of the dermis is undergoing calcification at its tip, whilst the stratum Malpighii over it is furnishing a crust of enamel, neither the "enamel-organ" nor the "dentine-papilla," if such they can be called, being markedly specialized nor different from the parts around them, save in contour and in the size of the epithelial cells.

He holds that the increased size &c. of the dermal spines over the surface of the jaws, where they constitute teeth, is adequately accounted for on the principle of increased use; that is to say, the excitation of pressure will bring about increased vascularity, and so forth.

His figures are very clear and accurate; and he has entered into the details of the process of calcification with

Teleostei.—Sections of the jaws of the Perch, Pike, Eel, Haddock, Cod, Mackerel, and Trout have been examined, and have been found to agree so closely in most points, that it is possible to embody the leading features of the process in a general description.

The literature of the subject may be disposed of in a very few words; in the first place, there is the view held by Professor Owen, and concisely expressed by him as follows:—"In all fishes the first step is the simple production of a soft vascular papilla from the free surface of the buccal membrane;" and "In many fishes, e. g. *Lophius*, *Esox*, the dental papillæ become buried in the membrane from which they rise, and the surface to which their basis is attached becomes the bottom of a closed sac;" and again, "Here, therefore, is represented the 'follicular' stage of the development of a mammalian tooth; but the 'eruptive' stage takes place without previous inclosure of the follicle and matrix in the substance of the jawbone." (Anatomy of Vertebrates, vol. i. p. 382.)

A much more accurate account of the process as it occurs in the mackerel is embodied in Professor Huxley's paper, already several times alluded to; the fact that the papilla is never free and that it is surmounted by an enamel-organ derived from and continuous with the oral epithelium is clearly laid down; and Kölliker mentions that the teeth of all osseous fish are developed in sacs not altogether from free papillæ. Nevertheless the exact nature of the process has not, so far as I know, been described by any previous author.

In all cases the whole series of changes take place beneath an unbroken surface, and often at some little depth; in this respect, however, differences are met with upon different bones in the mouth of the same fish, so that this would appear to be influenced by accidents of situation.

From the deepest layer of the oral epithelium, which is very thick in many fish, there dips downwards a blunt-ended process, descending into the loose connective tissue beneath. When it approaches the surface of the bone, a dentine-pulp is developed in the subjacent connective tissue, which it eventually covers over like a cap or bell-jar.

The epithelial process, making its way downwards, is recognizable before the dentine-papilla can be distinguished; its end becomes transformed into an enamel-organ, but no very definite capsule is formed around the dental germ.

There is therefore no "papillary" stage and no "follicular" stage, in the sense in which these terms are ordinarily used; the only appearance at all suggestive of the existence of free papillæ with which I am familiar is to be met with in the haddock, in which fish the tissues above a forming tooth-germ become elevated in places into a sort of papilla, which is, however, altogether external to and distinct from any part of the dental germ, which latter constitutes less than one third of its bulk and is far below its surface.

more minuteness than I have done. But I do not think that the grounds which he has adduced for asserting the existence of a membrana preformativa in the sharks are adequate to weigh against the reasons which have led Waldeyer and others to doubt its existence; and my own researches in this direction lead me to the belief, long ago expressed by my father, that the appearances described are susceptible of a different interpretation.

The general relationship of the dental germs to the oral epithelium, to the already formed teeth, and to the bone is shown in the perch in fig. 4, and in the sharp-nosed eel in fig. 6; the process in the two fish is so closely similar that it seems unnecessary to separately describe their tooth-germs.

An early stage is represented in fig. 7, in which the inward-growing epithelial process has formed an embracing cap or enamel-organ, but no calcification has as yet occurred. The enamel-cells are of very large size over the apex of the dentine-papilla, measuring about $\frac{1}{400}$ of an inch; but at a somewhat later stage (fig. 8) the large enamel-cells are seen to be confined to the immediate summit of the tooth, those a little further down (*e'* in the figure) being very much smaller ($\frac{1}{1000}$ of an inch). This same point is shown in the tooth-sac of a perch (fig. 5), in which the cells of the enamel-organ over the summit are large, but those extending down the sides of the tooth small and comparatively inconspicuous.

At a still later stage (fig. 9) the large cells on the apex have disappeared, and the whole enamel-organ consists of the smaller cells upon the sides of the dentine-cap, which are about $\frac{1}{1200}$ to $\frac{1}{1500}$ of an inch in length.

This peculiar configuration of the enamel-organ has relation to the partial disposition of the enamel upon the tooth; thus the tooth of the sharp-nosed eel (fig. 10) has a sharp conical cap of enamel upon its summit, the enamel being absent, or so thin that I cannot be sure of its existence, upon the sides of the tooth*.

We may thus say that we have exemplified within the boundaries of a single tooth-sac a functional and a rudimentary enamel-organ; and it is interesting to observe that the appearance of the rudimentary or lower portion of the enamel-organ closely resembles that of the entire rudimentary enamel-organ of the armadillo, which I have elsewhere described (Quart. Journ. Micros. Sci. 1874).

The fact that the development of the "enamel-cells" bears a direct relation to the thickness of the enamel to be formed also lends support to the view (which on other grounds I am strongly inclined to support) that the enamel is formed by the direct conversion of the enamel-cells into the hard tissue.

It is difficult otherwise to account for the contrast presented by the length of the cells in the different parts of the enamel-organ; and I may add that the aggregate length of the cells and the enamel cap already formed in fig. 8 just makes up the thickness of the enamel cap upon an average completed tooth.

* The existence of terminal caps of enamel, a character upon which alone Professor Owen has founded his fossil genus "*Ganacrodus*," is apparently by no means uncommon; I have found them in the eel, the perch, the newt, and the salamander; and as they are very easily lost in making sections, it is probable that they are present upon many teeth on which their presence has not as yet been demonstrated.

The positive determination of the absence of a thin layer of enamel upon the exterior of a tooth is a matter of no little difficulty, although it might at first sight appear easy enough: the double contour which is due to the thickness of the section can hardly be with certainty distinguished from a very thin structureless external layer, though the use of the dark-ground illumination will often bring the enamel layer out distinctly, owing to the difference in its refractive index. However, as I find the presence of an enamel-organ to be universal, the presence or absence of a merely rudimentary deposit of enamel ceases to be a fact of so much importance.

Of the dentine-germs or papillæ there is little to be said; they have a well-marked odontoblast layer, especially in the eel, and their bases contribute nothing to the formation of a special capsule. In fact the tooth-germs are only bounded by adventitious capsules, due to the condensation of the loose connective tissue around them. The enamel-organs long retain a connexion with the oral epithelium, which, however, becomes lost after a time, as by the elongation of the tooth its summit soon passes upwards into the substance of the oral epithelium; the "neck of the enamel-organ" is seen at *b* in figs. 5, 6, 7, 8, and 9.

The formation of new dental germs is perpetual, each enamel-germ being formed *de novo*, without being derived from any part of the earlier germs.

So far I can confirm the statements of Prof. OWEN, that "the germs of the new teeth are developed, like those of the old, from the free surface of the buccal membrane throughout the whole period of succession—a circumstance peculiar to the present class."

But I cannot agree in the further statement that "it is very conspicuous in the cartilaginous fishes, &c.;" for in these the enamel-organ of each new tooth is derived from a part of that of its predecessor, in a manner closely analogous to that observed by myself in reptiles, and by KÖLLIKER in the formation of the germ of the permanent teeth in man. To the manner of attachment of the teeth of the eel I may briefly allude, as it is shown in fig. 10, although I have already described it more fully elsewhere (Transactions of the Odontological Society, 1874). Each tooth is perched on the summit of a hollow bony column, into which its formative pulp extends for a short distance.

This little column of bone, which is specially developed for and renewed again after the loss of each tooth, is formed around the base of the tooth-pulp, which contracts below the point where dentine ceases to be formed.

The dentine ends sharply where the bone begins; not the smallest fusion of the two tissues appears to take place; and if we imagine dentine to be formed in the lower portion of the pulp, where it enters the hollow bony support, we should have a sort of rudimentary socket formed. This, however, never takes place in the eel: the dentine ends in a slightly rounded border at a point altogether above the bone.

The teeth of the perch, and indeed of many other fishes, are similarly attached; indeed I think the generalization may safely be laid down that in all cases a special development of "bone of attachment" takes place.

The tooth of the mackerel (fig. 13) is somewhat differently attached; it is developed in a furrow running round the thin edges of the jaws, and when it is completed and erupted it becomes attached to the permanent bony walls of that furrow by a development of little bony trabeculæ which bridge over the interval and so fix it in its place.

The development of the teeth of the mackerel does not in essential respects differ from that described in the eel and the perch, save that the situation of the tooth-germ is peculiar, as has already been mentioned (fig. 12).

The enamel-organ, which attains but a feeble development, was seen by Prof. HUXLEY to be continuous with the oral epithelium; to his description I have only to add that the first step towards the formation of a new tooth-germ is the budding inwards of the oral epithelium (which has been lost from the surface of the section figured).

The tooth-germs of the pike originate in precisely the same manner as those above described; but it is not unusual to see two tooth-germs of different age apparently destined to succeed to the same tooth, a thing which I have not observed in the haddock, the eel, or the perch.

The enamel-organ of the pike attains to a development intermediate between that of the mackerel and that of the eel or perch; from the regular appearance and considerable size of its component cells, which measure from $\frac{1}{1000}$ to $\frac{1}{800}$ of an inch, I should anticipate that a layer of enamel would be found upon its teeth, which is apparently the case, though it is not very thick.

Although the enamel-organs of all these fish consist primarily of two rows of cells, and traces of their original formation may be in places discerned, as at the base of the enamel-organ in fig. 11, yet that layer of columnar cells which goes by the name of the "enamel epithelium" so greatly preponderates that the outer layer is soon lost sight of.

No stellate reticulum separates these two layers in any fish or reptile with which I am acquainted.

There are many points of importance which I have not touched upon in this short and imperfect paper—such, for example, as the presence or absence of a basement membrane or membrana preformativa upon the dentine-papillæ, as well as the subsequent details of the process of calcification. My object has, however, been merely to give a general outline of the subject, which I hope at some future time to fill in with greater detail.

My examination of the process of the development of the teeth having been now extended to a considerable number of Mammals, Reptiles, Batrachians, and Fish, justifies me in drawing some general conclusions as to the structure of the tooth-germs, the more important of which may be summarized as follows:—

1. It is desirable to entirely abandon the terms "papillary," "follicular," and "eruptive" stage, inasmuch as these are hypothetical and arbitrary, and correspond to no serial conditions verified by observation.

2. In all animals the tooth-germ consists primarily of two structures, and two only—the dentine-germ and the enamel-germ.

The simplest tooth-germ never comprises any thing more. When a capsule is developed it is derived partly from a secondary upgrowth of the tissue at the base of the dentine-germ, partly from an accidental condensation of the surrounding connective tissue.

3. The existence of an enamel-organ is quite universal, and is in no way dependent upon the presence or absence of enamel upon the completed tooth, although the degree to which it is developed has distinct relation to the thickness of the future enamel.

The presence of an enamel-organ in the fœtal narwal has been described by Professor Turner (Journal of Anatomy and Physiology, 1873); its occurrence in a fœtal armadillo by myself (Quart. Journ. of Micros. Science, 1874); while in the present paper instances of its occurrence where little or no enamel is formed are noted.

4. So far as my researches go, a stellate reticulum, constituting a large bulk of the enamel-organ, is a structure confined to the Mammalia† (it is absent in the armadillo, and I should infer, from Mr. Turner's description, in the narwal).

5. As laid down by Professor Huxley and Professor Kölliker, the dentine-papilla is beyond all question a dermal structure, the enamel-organ an epithelial or epidermic structure.

As I believe it can be shown that the enamel is formed by an actual conversion of the cells of the enamel-organ, this makes the dentine dermal, and the enamel epidermic structures.

6. In *Teleostei* the new enamel-germs are formed directly from the oral epithelium, and are new formations arising quite independently of any portion of the tooth-germs of the teeth which have preceded them. In mammals and reptiles, and in some, at all events, of the Batrachia, new tooth-germs are derived from portions of their predecessors.

7. In all animals examined the phenomena are very uniform: a process dips in from the oral epithelium, often to a great depth; the end of the process becomes transformed into an enamel-organ coincidently with the formation of a dentine-papilla beneath it.

The differences lie rather in such minor details as the extent to which a capsule is developed; and no such generalization as that the teeth of fish in their development represent only an earlier stage of the development of the teeth of Mammalia can be drawn.

Description of the Plate.

PLATE 31*.

Fig. 1. Transverse section of the lower jaw of a young dogfish, *Scyllium canicula*.

To the right is seen the thecal protecting fold of mucous membrane, slightly displaced. Between this and the jaw is seen the chain of enamel-organs, which, if the parts were exactly *in situ*, would solidly fill up the whole interspace. The epithelium, where it passes across from the jaw to the thecal fold, between the third and fourth tooth, is torn across.

a. Oral epithelium.

b. Neck of enamel-organ connecting it with oral epithelium.

c. Special "bone of attachment."

† It is also to be found in the poison-canal of the partly calcified tooth-germs of poisonous snakes, as I have described and figured in a paper upon the development of poison-fangs, in course of publication in the Philosophical Transactions.

d. Dentine-papilla.
e. Enamel-organ.
e^1. Rudimentary portion of enamel-organ.
f (fig. 1). Point of passage of the oral epithelium across on to the thecal fold.
g. Cap of enamel.
h. Bone of jaw (or cartilage in figs. 1, 2, 3).
l. Formed dentine, or completed tooth.
sp. Dermal spines.

(The lettering applies to all the figures.)

Fig. 2. More highly magnified portion of the same section, showing the structure of the enamel-organs, the relation of the dentine-papillæ to the mucous membrane, and the manner of fixation of the teeth.

Fig. 3. Section of the lower jaw of a dogfish about 3 inches long. The continuity of the skin carrying dermal spines with the mucous membrane and its teeth is well seen.

Fig. 4. General view of the relations of the oral epithelium to the young tooth-sacs; three teeth in place, which have lost their enamel tips, are shown, while on the right the lip is seen in outline. From the lower jaw of a perch, × 30.

Fig. 5. Tooth-sac of a perch, showing the continuity of the oral epithelium with the enamel-organ, the large enamel-cells at the upper part of the latter, and its rudimentary lower portion, &c., × 70.

Fig. 6. Transverse section of the lower jaw of a sharp-nosed eel; for the sake of clearness the subepithelial connective tissue has been left out.

Fig. 7. Very young tooth-sac of an eel, × 100.

Fig. 8. Tooth-sac a little more advanced, in which more dentine and enamel have been formed: the aborting of the enamel-cells at the lower edge of the enamel-organ is noticeable, × 70.

Fig. 9. Tooth-sac yet more advanced, in which the terminal cap of enamel is complete, and the enamel-organ has almost disappeared at the upper end of the sac, × 30.

Fig. 10. Single tooth of a sharp-nosed eel, showing its enamel cap and its supporting hollow column of bone, × 20.

Fig. 11. Young tooth-sac of a pike, × 70.

Fig. 12. Section of the lower jaw of a mackerel. The young tooth-sac is seen to be lodged in a groove in the edge of the bone: the oral epithelium is lost over the surface of this groove, but the neck of the enamel-organ is distinguishable, × 40.

Fig. 13. Tooth of a mackerel, showing the peculiarity of the attachment of the perfected tooth, which is fixed in place by numerous slight trabeculæ of new bone, which unite it to the margins of the groove in the edges of the jaws, × 15.

XI. The Croonian Lecture.—*Preliminary Observations on the Locomotor System of Medusæ.* By George J. Romanes, *M.A., F.L.S., &c.* *Communicated by Professor* Huxley, *LL.D., Sec. R.S., &c.*

Received November 1,—Read December 16, 1875.

I. Structure and Movements of the Medusæ.

§ 1. *Structure of the Medusæ.*—Although it is not my intention in this preliminary notice to enter into the literature of my subject, it is nevertheless desirable to quote the well-known statements of Prof. L. Agassiz regarding the nature and distribution of the nervous system which he describes as occurring in the Medusæ. He says:—"There is unquestionably a nervous system in Medusæ, but this nervous system does not form large central masses to which all the activity of the body is referred, or from which it emanates. . . . . In Medusæ the nervous system consists of a simple cord, of a string of ovate cells, forming a ring round the lower margin of the animal, extending from one eye-speck to the other, following the circular chymiferous tube, and also its vertical branches, round the upper portion of which they form another circle. The substance of this nervous system, however, is throughout cellular, and strictly so, and the cells are ovate. There is no appearance in any of its parts of true fibres.

"I do not wonder, therefore, that the very existence of a nervous system in the Medusæ should have been denied, and should not be at all surprised if it were even now further questioned. I would only urge those interested in this question to look carefully along the inner margin of the chymiferous tubes, and to search there for a cord of cells of a peculiar ovate form, arranged in six or seven rows, forming a sort of string, or rather similar to a chain of ovate beads placed side by side and point to point, but in such a manner that the individual cells would overlap each other for one half, one third, or a quarter of their length, being from five to seven side by side at any given point upon a transverse section of the row; and would ask those who do not recognize at once such a string as the nervous system to trace it for its whole extent, especially to the base of the eye-speck, where these cells accumulate in a larger heap, with intervening coloured pigment forming a sort of ganglion; then, further, to follow it up along the inner side of the radiating chymiferous tubes which extend from the summit of the vault of the body, and to ascertain that here, again, it forms another circle round the central digestive cavity, from which other threads, or rather isolated series of elongated cells, run to the proboscis; they will then be satisfied that this apparatus, in all its complication, is really a nervous system of a peculiar structure and adaptation, with peculiar relations to the other systems of organs. . . . . and such a nervous system I

have already traced in all its details, as here described, in the genera *Hippocrene* (*Bougainvillia*), *Tiaropsis*, and *Staurophora*" *.

As my own observations on the histology of the Medusæ are not yet complete, I do not intend to publish them on the present occasion; but I may nevertheless be permitted to remark, with reference to the passage just quoted, that the conclusion so positively enunciated concerning the function of the structures described has always appeared to me, as it has appeared to biologists in general, a conclusion that is certainly unwarranted by the facts. As the learned Professor himself insists, the cells to which he so confidently attributes a nervous character represent "a peculiar type of the nervous system, a type different from all those types which have yet been recognized in the animal kingdom;" and this fact alone, one would think, ought to have inspired extreme caution in founding deductions upon such a basis regarding a question of such high importance as is that concerning the presence of a nervous system in the class Hydrozoa. Whatever effect, therefore, the present paper may have in deciding this question, or in confirming the deductions of Prof. Agassiz, I wish to state, as emphatically as I can, that in my opinion these deductions were decidedly premature, and that hitherto the only legitimate attitude of mind to adopt towards the much-vexed question as to the presence of nerves in Medusæ, is that which is thus tersely formulated by one of the greatest living authorities upon the group:—"No nervous system has yet been discovered in any of these animals" †.

[Postscript I.—Since this paper was presented to the Royal Society, Professor Huxley has been kind enough to direct my attention to an important memoir on the Medusæ, which I had not previously read. This memoir is by Prof. Haeckel ‡, and in it he assigns special importance to his careful researches into the histology of the nervous tissues. The following is an epitome of his results, so far as they bear upon the subject of the present paper.

After stating the conflicting views held by Agassiz, M'Crady, Fritz Müller, Leuckart, Keferstein, Ehlers, Claus, and others concerning the existence of a nervous system in Medusæ, Prof. Haeckel proceeds to state that his own observations with reference to this subject do not agree with those of any previous writers. These observations were chiefly made upon the *Geryonidæ*—a group of naked-eyed Medusæ which, according to this naturalist, present exceptionable facilities for demonstrating the presence of nervous elements by means of microscopical research. In their distribution these elements are described as forming a continuous circle all round the margin of the nectocalyx, following the course of the radial canals throughout their entire length, and proceeding also to the tentacles and to the marginal bodies. At the base of each tentacle there is

* Prof. L. Agassiz "On the Naked-eyed Medusæ of the shores of Massachusetts in their perfect state of Development:" see Memoirs of the American Academy of Arts and Sciences, new series, vol. iv. part ii. pp. 232, 233 (Cambridge and Boston: Metcalf and Co., 1850).

† Huxley, 'Classification of Animals.'

‡ Beiträge zur Naturgeschichte der Hydromedusen, von Dr. E. Haeckel (Leipzig, 1865).

a ganglionic swelling, and it is from these ganglionic swellings that the nerves just mentioned take their origin. The most conspicuous of these nerves are those that proceed to the radial canals and marginal vesicles, while the least conspicuous are those that proceed to the tentacles. Cells, as a rule, can only be discerned in the ganglionic swellings, where they appear as fusiform and distinctly nucleated bodies of great transparency and high refractive power. On the other hand, the nerves that emanate from the ganglia are composed of a delicate and transparent tissue, in which no cellular elements can be distinguished, but which is longitudinally striated in a manner very suggestive of fibrillation. Treatment with acetic acid, however, brings out distinct nuclei in the case of the nerves that are situated in the marginal vesicles, while in those that accompany the radial canals ganglion-cells are sometimes met with.

It will be seen from this brief *résumé* that Prof. HAECKEL's account of the distribution of the nervous tissues in Medusæ closely resembles that which had already been given by AGASSIZ, and from this it might be supposed that the one series of observations are confirmatory of the other. Prof. HAECKEL himself, however, is clearly of a very different opinion, and in several essential points his description certainly does not agree with that of AGASSIZ. For my own part, as I am able conscientiously to endorse all that Prof. HAECKEL says with regard to the extreme difficulty of distinguishing, in any of the species named by AGASSIZ, histological elements to which a nervous function might reasonably be assigned, I cannot help still thinking that the last-named observer must have been mistaken in his inferences concerning the tissue, which he says he observed without subjecting it to treatment of any kind. Possibly the structure which he describes may have been the optical expression of the thickness of the ectoderm in the region of the nutritive canals. Be this as it may, however, I cannot allow this postscript to appear without stating that in my opinion the microscopical researches of Prof. HAECKEL in this connexion are of much greater value than those of any previous observers; and this not only because of his deservedly high reputation as an histologist, but also because, judging from his figures, the tissues to which he ascribes a nervous function bear so close a resemblance to nervous tissue in general. Moreover, while this experienced microscopist is careful to state that even in the *Geryonidæ* it is no easy matter to distinguish the nervous elements, he also states (as already observed) that in this group these elements are much more readily distinguishable than in any other group of the naked-eyed Medusæ. For these reasons, therefore, I consider Prof. HAECKEL's deductions from anatomical structure to physiological function as of a more legitimate, and so of a more trustworthy, character than were those of Prof. AGASSIZ; and when they are taken in conjunction with the remarkable verification which they receive from the experiments to be detailed in this memoir, they ought, I think, to be regarded as finally decisive of the long-disputed question as to the presence of a nervous system in Medusæ.]

§ 2. *Movements of the Medusæ.*—It is of course known to every one that the Medusæ are naturally locomotive animals, the various species swimming more or less rapidly by means of an alternate contraction and dilatation of the entire swimming-organ. It may

not be so generally known, however, that these swimming-movements, although ordinarily rhythmical, are, at any rate in the case of some species, to a limited extent voluntary—using the latter term in the same sense as it is applicable to invertebrated animals in general. For instance, if *Sarsia* or *Aurelia*, &c. be *gently* irritated, the swimming-motions immediately become accelerated, and the acceleration persists for some time after the irritation has been withdrawn; but to secure this result the irritation must not be of such a character as an inanimate object might supply. Again, individuals belonging to some of the discophorous species of the naked-eyed Medusæ* exhibit peculiar movements on being alarmed; but I am not sure whether these are, as is most probable, purely involuntary, or performed with the view of affording protection to the more vital parts of the animal. Possibly the object may be to decrease the buoyancy of the nectocalyx, and so to escape from the source of injury by sinking through the water. In any case, however, it is necessary that I should here describe these movements, for I shall have occasion to refer to them later on. The movements in question, then, consist of a sudden folding together of the entire nectocalyx, consequent on an abnormally strong contraction of the swimming-muscles; and this contraction, besides being of unusual strength, is also of unusual duration. Thus the best idea of this movement will perhaps be gained by regarding it as a sort of spasm. The time during which this spasmodic contraction lasts is pretty uniform in different individuals of the same species; but it varies in different species from three to six seconds or more. In all cases the disappearance of the spasm is comparatively gradual, the nectocalyx re-expanding in a slow and graceful manner, instead of with the rapid motion characteristic of ordinary swimming. These movements only occur when the animal is being injured or threatened with injury.

II. Fundamental Observations.

§ 1. *Effects of excising the entire margins of Nectocalyces.*—Confining our attention under this heading to the naked-eyed Medusæ, I find that the following proposition applies to every species of the group which I have as yet had the opportunity of examining:—*Excision of the extreme margin of a nectocalyx causes immediate, total, and permanent paralysis of the entire organ.* Nothing can possibly be more definite than is this highly remarkable effect. I have made hundreds of observations upon various species of the naked-eyed Medusæ, of all ages and conditions of freshness, vigour, &c.; and I have constantly found that if the experiment be made with ordinary care, so as to avoid certain sources of error presently to be named, the result is as striking and decided as it is possible to desire. Indeed I do not know of any case in the animal kingdom where the removal of a centre of spontaneity causes so sudden and so complete a paralysis of the muscular system, there being no subsequent movements or twitchings of a reflex kind to disturb the absolute quiescence of the mutilated organism. The

* I adhere to Forbes's classification only because I have not happened to meet with any individual of the family Lucernariadæ.

experiment is particularly beautiful if performed on *Sarsia*; for the members of this genus being remarkably active, the death-like stillness which results from the loss of so minute a portion of their substance is rendered by contrast the more surprising.

From this experiment, therefore, I conclude that in the margin of all the species of naked-eyed Medusæ which I have as yet had the opportunity of examining there is situated an intensely localized system of centres of spontaneity, having at least for one of its functions the origination of impulses to which the contractions of the nectocalyx, under ordinary circumstances, are exclusively due. And this obvious deduction is confirmed (if it can be conceived to require confirmation) by the behaviour of the severed margin. This continues its rhythmical contractions with a vigour and a pertinacity not in the least impaired by its severance from the main organism; so that the contrast between the perfectly motionless swimming-bell and the active contractions of the thread-like portion which has just been removed from its margin is as striking a contrast as it is possible to conceive. Hence it is not surprising that if the margin be left *in situ* while other portions of the swimming-bell are mutilated to any extent, the spontaneity of the animal is not at all interfered with. For instance, if the equator of any individual belonging to the genus *Sarsia* (fig. 1, p. 276) be cut completely through, so that the swimming-bell instead of being closed at the top is converted into an open tube, this open tube continues its rhythmical contractions for an indefinitely long time, notwithstanding the organism so mutilated is, of course, unable to progress. Thus it is a matter of no consequence how small or how large a portion of contractile tissue is left adhering to the severed margin of the swimming-bell; for whether this portion be large or small, the locomotor centres contained in the margin are alike sufficient to supply the stimulus to contraction. Indeed if only the tiniest piece of contractile tissue be left adhering to a single eye-speck cut out of the bell of *Sarsia*, this tiny piece of tissue in this isolated state will continue its contractions for hours or even for days.

This observation, then, on the effect of removing the extreme periphery of nectocalyces, as it undoubtedly demonstrates the presence of an intensely localized system of locomotor centres in at least some of the Medusæ, and as it thus opens the way for a great amount of further experimental research—this observation I shall afterwards speak of as the fundamental observation. I very much regret to say, however, that, in consequence of my having been this year engaged in another line of experimental research which necessitated my constant residence in one locality, I have hitherto been able to make this fundamental observation only in the case of six genera of the naked-eyed Medusæ. As yet, therefore, it would be premature to predict with much confidence that subsequent experiments will prove the locomotor centres to be equally localized in the case of all the naked-eyed Medusæ. Nevertheless, as the genera which I have already submitted to the simple operation just described are genera which happen to present the most extreme differences as to form, size, and structure that occur among the true Medusæ, I think my results afford very good analogical grounds for expecting that future researches will prove the exclusive localization of spontaneity in the marginal

rim of nectocalyces to be as constant a feature in the anatomy of true Medusæ as is the presence of the polypite, the tentacula, or the nutritive canals*.

Exception.—I must here record one exception to the numberless instances in which excision of the margins of naked-eyed Medusæ caused paralysis of the nectocalyces. This single exception occurred in a species called *Staurophora laciniata*, a species which, as I shall afterwards explain, I have made the subject of an investigation that necessitated the removal of the margins as the first step in each experiment. I have therefore removed the margin from scores of individuals belonging to this species, and have never met with any but this one exception to the general rule.

In this one exceptional case, after the entire margin had been removed, there were still three distinct centres of spontaneity remaining. One of these centres was situated in the muscular tissue near the periphery of the nectocalyx, and the other two in the substance of the greatly extended polypite that is characteristic of this animal, one centre being placed in each of the two opposite arms of the cross. On carefully excising these three points, with as small a portion of tissue adhering to them as possible, entire cessation of movement ensued in the nectocalyx, while the three severed parts persisted in their rhythmical contractions as long as I continued to observe them. Regarding this exception I have only to remark that it occurred in a somewhat aberrant form of the true Medusæ, and one which, in the unusual size of its nectocalyx, approached that which is usual in the swimming-organs of the covered-eyed Medusæ. It may also be observed that, looking to the type of animal life presented by the order, occasional exceptions of this kind might be expected to occur; and I am only surprised that within my experience they have proved themselves so rare.

§ 2. *Effects of excising the entire margins of Gonocalyces*†.—Turning now to the covered-eyed division of the Medusæ, I find, in all the species I have come across, that excision of the margins of gonocalyces produces an effect analogous to that which is produced by excision of the margins of nectocalyces. There is an important difference, however, between the two cases, in that the paralyzing effect of the operation on gonocalyces is neither so certain nor so complete as it is on nectocalyces. That is to say, although in the majority of experiments such mutilation of gonocalyces is followed by immediate paralysis, this is not invariably the case; so that one cannot here, as with the naked-eyed Medusæ, predict with any great confidence what will be

* The following are the species of naked-eyed Medusæ on which I have made the fundamental observation:—*Sarsia tubulosa* (Sars); *S. pulchella* (Forbes); *S. erythrops* (Romanes); *Thaumantias inconspicua* (Forbes); *Bougainvillia* (*Hippocrene*) *superciliaris* (Agassiz); *B. gigantea* (?) (Romanes); *B. fruticosa* (?) (Romanes); *Staurophora laciniata* (Agassiz); *Tiaropsis diademata* (Agassiz); *T. indicans* (Romanes); *T. polydiademata* (Romanes); *T. oligoplocama* (Romanes); *Stomabrachium octocostatum* (Sars).

† Although not in accordance with general usage, I extend this term to denote the swimming-organ of a covered-eyed Medusa. I do so because those terms which are more properly applicable to this structure are by some authors employed indiscriminately to designate the swimming-organs both of the covered- and of the naked-eyed divisions. Therefore, as it is most desirable for the purposes of the present memoir to avoid any ambiguity in this matter, I trust I shall be excused for thus violating the accepted terminology.

the immediate result of any particular experiment. Further, although such mutilation of a gonocalyx is usually followed by a paralysis as sudden and marked as that which follows such mutilation of a nectocalyx, the paralysis of the former differs from the paralysis of the latter in that it is very seldom *permanent*. After periods varying from a few seconds to half an hour or more, occasional, weak, and unrhythmical contractions begin to manifest themselves; or the contractions may even be resumed with but little apparent change in their character and frequency. The condition of the animal before the operation as to general vigour, &c. appears to be one factor in determining the effect of the operation; but this is very far from being the only factor.

These remarks apply to gonocalyces in general. It must now be observed, however, that these remarks do not apply in equal degrees to all the genera of the covered-eyed Medusæ which I have examined. In other words, if a number of individuals in each of several genera be subjected to the operation we are considering and the results tabulated, it will be found that the average degree of paralysis manifested by the individuals of the different genera is not uniform. For the sake of brevity, therefore, I shall choose a species belonging to each of the two genera which, within my limited experience, have shown the greatest differences in this respect; and by giving a somewhat detailed account of the manner in which the individuals composing these species behave under the form of mutilation described, I shall hope to convey a general idea of the manner in which individuals composing all the other species I have examined behave under similar circumstances—it being understood that all the other species I have examined occupy, in the particulars we are concerned with, a position somewhere intermediate between the two extremes which are described.

The species, then, to which I allude are *Aurelia aurita* and *Cyanœa capillata*, both exceedingly common forms. Of these species the first approaches nearest to the naked-eyed Medusæ in the concentration of its locomotor centres into the margin of the swimming-organ, while the second departs most widely from the naked-eyed Medusæ in this respect. It must be carefully noted, however, that in the case of these species, as well as in that of all the other species of covered-eyed Medusæ I have examined, the individual variations in these particulars are very great. Therefore, while describing these individual variations in the cases of *Aurelia aurita* and *Cyanœa capillata*, I wish it to be understood that the same remarks apply to all the species of the covered-eyed Medusæ which I have observed.

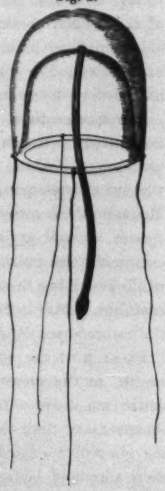
Excision of the entire margin of *Aurelia aurita*, inclusive of course of lithocysts, causes, in the great majority of cases, instantaneous and complete paralysis of the entire gonocalyx. In the minority of cases one or more supernumerary locomotor centres assert their presence in some part or parts of the general contractile tissue of the gonocalyx *immediately* after removal of its margin. The first of these two divisions admits of being again divided into two subdivisions. In the cases composing one of these subdivisions (and these are much the more numerous) additional centres of spontaneity become, so to speak, developed after the lapse of a greater or less

interval of time; so that one cannot be quite sure, even for an hour after the operation, that the paralysis, however complete up to that time, will prove itself permanent. In the cases composing the other of these subdivisions, the paralysis, besides being instantaneous and complete, is also permanent, and thus in every way resembles the paralysis caused by the fundamental experiment in the case of nectocalyces.

Excision of the entire margin of *Cyanæa capillata* causes, in the majority of cases, instantaneous and complete paralysis of the gonocalyx; but this result is not of such comparatively frequent occurrence as it is with *Aurelia aurita*. Moreover, in the cases where supernumerary centres do not assert themselves immediately after the operation, they are almost sure to do so if the mutilated gonocalyx be left sufficiently long to recover from the shock caused by the operation. The period required before the first spontaneous contraction is given in such cases varies from a few minutes to an hour or more; but it is observable that if this period be prolonged, the subsequent contractions are almost sure to be of a feeble character with immensely long intervals between their occurrence—perhaps only one contraction being given in ten minutes or more, instead of between twenty to thirty contractions in one minute, as is characteristic of the unmutilated animal.

Upon the whole, then, although in all the species of covered-eyed Medusæ which I have as yet had the opportunity of examining the effects which result from excising the margins of gonocalyces are such as to warrant me in saying that the main supply of locomotor centres appears to be usually situated in that part of these organs, these effects are nevertheless such as to compel me at the same time to conclude that the locomotor centres of the covered-eyed Medusæ are more diffused or segregated than are those of the naked-eyed Medusæ. Lastly, it should be stated that all the species of covered-eyed Medusæ resemble all the species of naked-eyed Medusæ in that their members will endure any amount of section it is possible to make upon any of their parts, other than their margins, without their spontaneity being in the smallest degree affected.

Fig. 1.



Sarsia, × 3 times.

§ 3. *The effects of excising certain portions of the margins of Nectocalyces.*—The next question which naturally presents itself is as to whether the locomotor centres are equally distributed all round the margin of a swimming-organ, or situated only, or chiefly, in the so-called marginal bodies. To take the case of the naked-eyed Medusæ first, it is evident that in most of the genera, in consequence of the intertentacular spaces being so small, it is impossible to cut out the marginal bodies without at the same time cutting out the intervening portions of the margin. The genus *Sarsia*, however, is admirably adapted (as a glance at the annexed figure will show) for trying the effects of removing the

marginal bodies without injuring the rest of the margin, and *vice versâ*. The results of such experiments upon members of this genus are as follow.

Whatever be the condition of the individual operated upon as to freshness, vigour, &c., it endures excision of three of its eye-specks without suffering any apparent detriment; but in most cases, as soon as the last eye-speck is cut out, the animal falls to the bottom of the water quite motionless. If the subject of the experiment happens to be a weakly specimen it will perhaps never move again: it has been killed by something very much resembling nervous shock. On the other hand, if the specimen operated upon be one which is in a fresh and vigorous state, its period of quiescence will probably be but short; the nervous shock (if we may so term it), although evidently considerable at the time, soon passes away, and the animal resumes its motions as before. In the great majority of cases, however, the activity of these motions is conspicuously diminished.

The effect of excising all the marginal tissue from between the eye-specks and leaving the latter untouched is not so definite as is the effect of the converse experiment just described. Moreover allowance must here be made for the fact that in this experiment the principal portion of the "veil" is of necessity removed; so that it becomes impossible to decide how much of the enfeebling effect of the section is due to the removal of locomotor centres from the nectocalyx, and how much to a change in the merely mechanical conditions of the organ. From the fact, however, that excision of the entire margin of *Sarsia* produces total paralysis, while excision of the eye-specks alone produces merely partial paralysis, there can be no doubt that both causes are combined. Indeed it has been a matter of the greatest surprise to me how very minute a portion of the intertentacular marginal tissue is sufficient, in the case of this genus, to animate the entire nectocalyx. Choosing vigorous specimens of *Sarsia*, I have tried, by cutting out all the margin besides, to ascertain how minute a portion of intertentacular tissue is sufficient to perform this function, and I find that this portion may be so small as to be quite invisible without the aid of a powerful lens. As it not unfrequently happens that in cutting out the extreme margin of *Sarsia* a minute part of the intertentacular tissue is left behind accidentally, I may here caution any one who repeats the fundamental observation upon this genus to be very careful in removing every atom of the marginal canal.

From numerous observations, then, upon *Sarsia*, I conclude that in this genus (and so, from analogy, probably in all the other genera of the true Medusæ) locomotor centres are situated in every part of the extreme margin of a nectocalyx, but that there is a greater supply of such centres in the marginal bodies than elsewhere.

§ 4. *Effects of excising certain portions of the margins of Gonocalyces.*—Coming now to the covered-eyed Medusæ, I find that the concentration of the locomotor centres of the margin into the marginal bodies, or lithocysts, is still more decided than it is in the case of *Sarsia*. Taking *Aurelia aurita* as a type of the group, I cannot say that,

either by excising the lithocysts alone or by leaving the lithocysts *in situ* and excising all the rest of the marginal tissue, I have ever detected the slightest indications of locomotor centres being present in any part of the margin of the gonocalyx other than the eight lithocysts; so that all the remarks made upon this species in § 2, while we were dealing with the effects of excising the entire margin of gonocalyces, are equally applicable to the experiment we are now considering, viz. that of excising the lithocysts alone. In other words, but for the sake of symmetry I might as well have stated at the first, that in the case of *Aurelia aurita* all the remarkable paralyzing effects which are obtained by excising the entire margin of a gonocalyx are obtained in exactly the same degree by excising the eight lithocysts alone: the intermediate marginal tissue, in the case of this species, is totally destitute of locomotor centres.

I have in this section chosen *Aurelia aurita* as the type of the covered-eyed Medusæ, because, from the flattened shape of its gonocalyx, the differential experiment of cutting out lithocysts and intermediate marginal tissue respectively admits of being conducted in a fairer way than in the case of any other species of the group I have happened to come across; for, in the case of these other species, the form of the gonocalyces necessitated excision of large masses of contractile substance before all the tissue included between the lithocysts could be wholly removed. It therefore became impossible for me in these cases to determine how much of the paralyzing effect was due to removal of locomotor centres, and how much to possibly general shock. But although I was thus precluded from making any trustworthy experiments upon the effect of cutting out all the marginal tissue from between the lithocysts of these species, I was of course able to perform the converse experiment of cutting out the lithocysts alone. The result of numerous experiments of this kind is to satisfy me that, in all the species of covered-eyed Medusæ I have examined, the *chief* marginal supply of locomotor centres is aggregated in the eight lithocysts, although I am unable, for the reasons just given, to say whether or not the *exclusive* marginal supply of these centres is so aggregated. From this it will readily be gathered that, in all the species of covered-eyed Medusæ I have examined, the paralyzing effects of excising the lithocysts alone are most strongly marked, although, of course, from what has been said upon this group in § 2, it will be understood that the experimenter must be prepared to meet with all grades of individual variations in this respect. With regard to specific differences, it will now be apparent that *Aurelia aurita* is, of all the forms I have examined, the one that is most strongly affected by removal of its lithocysts, the paralysis of the gonocalyx thus caused being, in some cases, as permanent as it is total. In all the other species of covered-eyed Medusæ examined, I have found it a very rare thing to obtain permanent paralysis by excision of lithocysts. It may here be added that a portion of any size of contractile tissue left adhering to an excised lithocyst of any species of covered-eyed Medusa will very frequently be found to continue its rhythmical contractions after its severance from the main organism,

while such is very rarely the case with any other portions of the marginal tissue when excised.

As the question concerning the presence of a nervous system in Medusæ has long been a warmly disputed one, it may perhaps facilitate its solution if I here observe that there is certainly no case in the whole animal kingdom where there is so great a disproportion between the mass of a ganglionic centre and that of the system which it is capable of setting in motion, as there is between the mass of a lithocyst and that of the gonocalyx which it animates. Thus, in order to obtain the exact proportions in the case of a medium-sized covered-eyed Medusid, weighing thirty pounds, I first removed seven of the lithocysts, and then observed that the eighth one continued to supply contractile impulses to the entire gonocalyx. I next cut out this lithocyst also, and having cleared it as much as possible of the adherent gelatinous tissue, weighed it. Observing further that the mutilated gonocalyx did not move for an hour after the operation (although previous to the operation it had been in active motion), I weighed this also, and obtained the surprising result, that the lithocyst had previously been animating a structure more than thirty million times its own weight!*

§ 5. *Summary of Division II.*—With a single exception to hundreds of observations upon six widely divergent genera of naked-eyed Medusæ, I find it to be uniformly true that removal of the extreme periphery of the animal causes instantaneous, complete, and permanent paralysis of the locomotor system. In the genus *Sarsia* my observations point very decidedly to the conclusion that the principal locomotor centres are the eye-specks, but that, nevertheless, every microscopical portion of the intertentacular spaces of the margin is likewise endowed with the property of originating locomotor impulses.

In the covered-eyed division of the Medusæ I find that the *principal* seat of spontaneity is the margin, but that the latter is not, as in the naked-eyed Medusæ, the *exclusive* seat of spontaneity. Although in the vast majority of cases I have found that excision of the margin impairs or destroys the spontaneity of the animal for a time, I have also found that the paralysis so produced is very seldom of a permanent nature. After a variable period occasional contractions are usually given, or in some cases the contractions may be resumed with but little apparent detriment. Considerable differences, however, in these respects are manifested by different species, and also by different individuals of the same species. Hence, in comparing the covered-eyed group as a whole with the naked-eyed group as a whole, so far as my observations extend I should say that the former resembles the latter in that its representatives usually have their main supply of locomotor centres situated in their margins, but that it differs from the latter in that its representatives usually have a greater or less supply of their locomotor centres scattered through the general contractile tissue of their swimming-

* This individual belonged to the species *Chrysaora hysoscella*. From analogy, however, I doubt not that if I had left the animal over night, next morning it would have exhibited feeble signs of spontaneity; for, as already observed, I have found it a rare thing to obtain thorough and *permanent* paralysis in any species of the covered-eyed Medusæ by the excision of lithocysts.

organs. But although the locomotor centres of a covered-eyed Medusa are thus, generally speaking, more diffused than are those of a naked-eyed Medusa, *if we consider the organism as a whole*, the locomotor centres in the *margin* of a covered-eyed Medusa are *less* diffused than are those in the *margin* of a naked-eyed Medusa; for, so far as my observations extend, I find that excision of the marginal bodies alone produces a greater comparative effect in the covered-eyed genera of Medusæ than it does in the genus *Sarsia*. But of course it is needless to say a much wider basis of observation than mine is required to establish this fact as applicable to the whole of the two groups of Medusæ. I may state, however, quite decidedly that in at least one species of the covered-eyed group (viz. *Aurelia aurita*) the only portions of the margin which are capable of originating spontaneous impulses to contraction are the eight lithocysts, and that in a very large majority of individuals belonging to this species excision of these minute bodies causes instantaneous and complete paralysis of the entire gonocalyx, which paralysis is sometimes also permanent*.

III. Stimulation.

§ 1. *Mechanical Stimulation.*—So far as my observations extend, I find that all Medusæ, after removal of their locomotor centres, invariably respond to every kind of stimulation. To take the case of *Sarsia* as a type, nothing can possibly be more definite than is the single sharp contraction of the mutilated nectocalyx in response to every nip with the forceps. The contraction is precisely similar to the ordinary ones that are performed by the unmutilated animal; so that by repeating the stimulus a number of times, the nectocalyx, with its centres of spontaneity removed, may be made to progress by a succession of contractions round and round the vessel in which it is contained, just as a frog, with its cerebral hemispheres removed, may be made to hop along the table in response to a succession of stimulations. The same remarks apply to all the species of covered-eyed Medusæ I have examined (though some species are more sensitive to stimulation than others): but in the case of many of the discophorous species of naked-eyed Medusæ these remarks must be somewhat modified; for, as previously stated, many of these species upon being irritated while still in an unmutilated state exhibit movements of a peculiar character quite distinct from the ordinary locomotor contractions; and now it must be added that in the case of all these species the mutilated nectocalyx does not, as in *Sarsia* and the covered-eyed Medusæ, respond to a strong stimulus by a single locomotor contraction (although they may do so in response to a weak stimulus), but it performs other actions that differ in different

* Although not covered by the title of this paper, it is desirable here to state that neither in the naked- nor in the covered-eyed Medusæ is the *polypite* affected in the smallest degree as to its motions by excision of the margin of the swimming-organ. For hours and days after the latter, in consequence of this operation, has entirely ceased to move, the former continues to perform whatever motions are characteristic of it in the unmutilated organism. Indeed these motions are not at all interfered with even by a complete severance of the polypite from the rest of the animal. In many of the experiments subsequently to be detailed, therefore, I began by removing the polypite, in order to afford better facilities for manipulation.

species, the action, however, in any given case always precisely resembling that which the unmutilated nectocalyx would have performed if irritated in the same way. Now *Sarsia*, in common with all the covered-eyed genera examined, when in the unmutilated state always endeavours to swim away from a source of irritation or alarm, and never performs any other motions; so that all the cases conform to this one simple rule:—*Every Medusa, when its centres of spontaneity have been removed, responds to a single stimulation by once performing that action which it would have performed in response to that stimulation had its centres of spontaneity still been intact.*

Different species of Medusæ exhibit different degrees of irritability in responding to stimuli; but in all the cases I have met with the degree of irritability is remarkably high. Thus *Aurelia aurita* is perhaps, of all the species I have experimented upon, the least sensitive to stimulation; yet if a narrow strip of tissue without any centres of spontaneity be taken from this animal and made to support in the air the weight of another strip which is spontaneously contracting, the slight amount of friction caused by the one gelatinous surface passing over the other upon each contraction of the uppermost strip is sufficient to determine a responsive contraction in the undermost strip. In some of the other species of covered-eyed Medusæ I have seen responsive contractions of the whole gonocalyx follow upon the exceedingly slight stimulus caused by a single drop of sea-water let fall upon the irritable surface from the height of one inch.

§ 2. *Electrical Stimulation* (A).—All parts of all the Medusæ I have examined are highly sensitive to electrical stimulation, both of the constant and of the induced currents. There is thus a large field for experimental research here opened up, and one upon which I have bestowed a considerable amount of labour. In now giving an abstract of some of the results hitherto yielded, it is only right that I should take the opportunity thus afforded of expressing my obligations and sincere thanks to my learned and highly esteemed friend Prof. Burdon-Sanderson, but for whose prompt kindness in sending me all the electrical and various other apparatus in immediate answer to my numerous requests, it would have been impossible for me this year to have conducted, with any kind of completeness, the investigation which I undertook.

As just stated, both the severed margin, or system of locomotor centres, and the swimming-organ from which these have been removed respond to stimulation both of the direct and of the induced currents. There is an important difference, however, between the behaviour of the severed margin and of the mutilated nectocalyx with reference to these two kinds of stimulation; for while the former shows itself more sensitive to the induced shock than to the direct current, the reverse is true of the latter. That is to say, while the severed margin continues responsive even to weak induction-shocks after it has ceased to be affected either by make or break of the direct current, the mutilated nectocalyx continues responsive to make and break of the direct current after it has ceased to respond to the strongest induced shock, or even to Faradaic electricity with the secondary coil pushed to zero (one Daniell's cell in all

cases). It is needless to observe how strongly this fact points to the ganglionic nature of the locomotor centres in the marginal tissues of Medusæ.

My observations were principally made upon the genus *Sarsia*; and the method I employed was to pass the platinum electrodes into the concavity of the mutilated swimming-bell while the latter was in the water, and then gently to raise the former until the contact between them and the tissue was seen to be sufficiently intimate. Similarly of course with the severed margin. I may here remark, for the benefit of those who may repeat this observation, that when the constant current is being applied to the mutilated bell the latter often contracts in a somewhat rhythmical manner. This is perhaps due to the hydrogen bubbles acting as stimulants to contraction, and in any case is certainly not to be regarded as *spontaneous* action. I may also state that minute crustaceans, by striking the mutilated bell, sometimes supply a stimulus to contraction. It is therefore desirable to conduct these experiments in filtered sea-water; and the same precaution of course should be taken when conducting the fundamental observation upon such swimming-organs as prove themselves highly sensitive to stimulation after removal of their locomotor centres.

(B) *Excitable tracts.*—The extreme sensitiveness of all the tissues of all the Medusæ to electrical stimulation affords us the means of ascertaining whether there is any localization of definite excitable tracts in these animals. As *Sarsiæ* are the most active of the Medusæ, and likewise the most delicately sensitive to electricity*, I have in this, as in other cases, taken the genus as the type of the group, and made it the subject of a more careful investigation than any of the other genera. In this preliminary paper, therefore, I shall confine myself, under this heading, to detailing my observations upon the genus *Sarsia* alone. The method I adopted was to slit open one side of the swimming-bell from base to apex, and then to lay it flat upon a glass slide with its inner surface uppermost. Having either cut off or turned back the polypite, I then placed the entire animal under the microscope on a slightly grooved object-glass, where I could keep it alive for a considerable time by moistening it at intervals with drops of sea-water. The stimulus I employed was always the induction-shock supplied by a single Daniell's cell and Du Bois-Reymond's coil. The electrodes were fine needles passed through a small piece of india-rubber. The latter was firmly fixed to the stage forceps, which in turn was firmly fixed to a mechanical stage. In this way the object and the electrodes could be moved in any direction without altering their relative positions—a provision which made all the difference between the following observations being possible or impossible; for without this provision it would not have

* At whatever point the bell of *Sarsia* first responds to the induction-shock, it will generally be found that drawing out the secondary coil a quarter, or even an eighth, and very often only a sixteenth of an inch will make all the difference between a vigorous response and no response. Moreover this delicacy of appreciation, besides being thus very great, is also very constant: the excitability of the tissue is seldom found to vary in the least degree for a tolerably long time, although, of course, under the unnatural conditions in which the animal is placed, the excitability of its tissues begins at last gradually to diminish.

been practicable to get the electrodes adjusted accurately upon the various minute histological tracts of tissue, and at the same time to get them within the field of the microscope. The power I used was one-inch Ross, and the strength of the induction-shock was of course regulated in the ordinary way.

The following are the results yielded by this method of investigating the distribution of excitable tracts in *Sarsia*; and it is interesting to observe how uniformly they coincide with the results obtained by section. I should like to observe, however, that some of the observations are attended with considerable difficulty (arising from escape of the current, conductivity of the gelatinous tissue, &c.); so that, although I have spent a great deal of time and trouble over this part of the inquiry, I desire it to be understood that I intend to confirm these observations more extensively next year.

The apex of the swimming-bell of *Sarsia* is much the least excitable portion of the animal; and from this point downwards to the margin there is a beautiful and uninterrupted progression of excitability, the latter being greatest of all when the electrodes are placed upon the string of cells described by Agassiz as nerve-cells. The actual proportions in one average case were as follow:—

(i) Electrodes on apex of inner bell. No contraction on strongest shock.

(ii) Electrodes a quarter of an inch from margin. Bell first contracted with secondary coil at 2 centims.

(iii) Electrodes one eighth of an inch from margin. Bell first contracted with secondary coil at 3 centims.

(iv) Electrodes one sixteenth of an inch from margin. Bell first contracted with secondary coil at 5 centims.

(v) Electrodes on the marginal canal. Bell first contracted with secondary coil at 9 centims.

Of the marginal tract of excitable tissue, the degree of excitability differs slightly in different parts. It is least when the electrodes are placed midway between the two eye-specks; it is somewhat greater when an eye-speck is included between the electrodes. The excitability is again slightly higher when one electrode is placed in an eye-speck and the other outside it. Still greater is the excitability when both electrodes are put into one eye-speck; and the excitability is greatest of all when care is taken to place both electrodes in that half of the eye-speck which is above the pigment-spot. In these remarks of course I wish it to be understood that the excitability is greater in the parts named than in other parts, when an equal amount of tissue is included between the electrodes in the case of both experiments constituting any comparative observation. The following are the ratios in an average case:—

(i) Electrodes between two eye-specks. Bell first contracted at $6\frac{1}{2}$ centims.
(ii) Electrodes with one eye-speck between them. Bell first contracted at $7\frac{1}{2}$ centims.

(iii) Electrodes with one eye-speck between them. Bell first contracted at 7 centims.
(iv) One electrode in an eye-speck. Bell first contracted at 8 centims.

(v) Both electrodes just outside an eye-speck. Bell first contracted at 8 centims.
(vi) Both electrodes in the eye-speck. Bell first contracted at 10 centims.

(vii) Both electrodes in the pigment part of an eye-speck. Bell first contracted at 8 centims.

(viii) Both electrodes in the vesicular part of an eye-speck. Bell first contracted at 12 centims.

With regard to the other parts of the nectocalyx, I have merely to state that there is a marked difference between the excitability of this organ when the electrodes are placed upon any one of the four radiating canals (and so upon the ascending nerve-chains described by Agassiz) and when the electrodes are placed upon the tissue between any of the canals. The ratio is generally about 9 centims. : $6\frac{1}{2}$ centims.

Thinking that this greater excitability of the bell when the electrodes were placed upon one of the radiating canals than when they were placed upon the intermediate tissue might possibly have been due to a slight escape of electricity, which in the one case would have become diffused over the muscular tissue of the bell, while in the other it might have been conducted to the marginal centres by a possibly high conducting-power of the radiating canal, I took the precaution of removing the margin altogether; but this did not modify the results.

I conclude, therefore, that in almost every particular there is, in the case of *Sarsia*, a perfect coincidence between the microscopical observations of Prof. L. Agassiz and the results yielded by the method of exploration by stimulus just described. Nevertheless I may here repeat what I said in the opening section, viz. that the inference so confidently drawn by that observer as to the function of the histological element he described was, as an inference, decidedly premature*.

(C) I must now describe a mode of section which would naturally fall under the next division of my subject, were it not for its great value in enabling us to conduct an important part of the inquiry relating to electrical stimulation.

* It is worth while to observe also, as showing the danger of drawing conclusions concerning function from histological observation alone, that although Prof. Agassiz was so positive regarding the localization of nervous tissue in the margins of Medusæ, he had no idea that the function of this supposed nervous tissue was so intensely specialized,—witness the passage already quoted, "There is unquestionably a nervous system in Medusæ, but this nervous system does not form large central masses to which all the activity of the body is referred, or from which it emanates."

There is another remark which may here be made. Prof. Agassiz somewhere observes that it is noteworthy how, in the naked-eyed Medusæ, the supposed nervous tracts follow everywhere the course of the nutritive system. Now, as my method of exploration by stimulus has yielded results confirmatory of Prof. Agassiz's views in this respect, it becomes worth while to speculate as to whether the greater diffusion of the centres of spontaneity in the covered-eyed than in the naked-eyed group of Medusæ may not stand in some relation to the characteristically greater diffusion of the nutritive system in the one group than in the other. Certain it is that lithocysts always appear to stand in some peculiar anatomical relation to the nutritive canals, the latter sweeping round to meet the former (see Plate 32) and communicating through them with the external water. This, of course, may only be due, as Gegenbaur supposes, to the lithocysts having some excretory function to perform; but now that these organs have been raised to the dignity of locomotor centres, and analogous centres have been proved to be similarly associated with nutritive tracts in the naked-eyed Medusæ, it is well to remember, in view of some deductions from the general theory of evolution, that this possibly non-accidental association of nutritive systems with the earliest indications of nervous systems may turn out to be an association of no small significance.

The mode of section is a very simple one, consisting merely in cutting round a greater or less extent of the marginal tissue, leaving one end of the resulting strip free and the other end attached *in situ*. Upon now irritating the distal or unattached end of this marginal strip, a wave of contraction may invariably be seen to start from the point at which the irritation is applied, and with some rapidity to traverse the entire strip. Upon arriving at the proximal or attached end of the strip, this contractile wave delivers its influence into the swimming-organ, which thereupon contracts in exactly the same manner as it does when itself directly irritated. Of course spontaneous contractions are continually originating in some portion or other of the severed strip; and these give rise to contractile waves and to contractions of the nectocalyx, just in the same way as do the disturbances originated by stimulus. In those species, however, of the discophorous naked-eyed Medusæ which respond to stimulation by the peculiar spasmodic movements of the nectocalyx already described, the difference between the effects upon the nectocalyx of contractile waves that originate spontaneously in the severed strip and those that thus originate in answer to stimuli is of a very marked character; for the spasmodic movements of the nectocalyx are as easily and as certainly evoked by irritating any part of the severed strip, as they are by irritating the substance of the nectocalyx itself.

From this description it will easily be seen that a Medusa thus operated upon supplies all the essential conditions for conducting the most important part of the investigation, so far as electrical stimulation is concerned, viz. that relating to electrotonus. We have already obtained ample evidence to warrant us in concluding that, if the organization of the Medusæ presents us with any thing that is analogous to nervous tissue at all, the periphery of the swimming-organ must be the position in which it is chiefly localized; so that even if these animals possess but the rudiments of a nervous system, a Medusa, when subjected to the mode of section just described, is for all practical purposes a nerve-muscle preparation.

If the intention of the experimenter be merely that of producing contractile waves, it does not signify upon what species of Medusa the form of section just described is practised; for whatever species happens to be chosen, the experiment is sure to be successful. But when the object in view is that of electrotonic investigation, it is desirable to exercise the utmost discretion in the choice of a suitable species. The one I have found most suitable is *Staurophora laciniata*; for this form presents all the qualities the experimenter can desire. Its size is sufficient to yield a foot or more of marginal tissue whereon to cause and test for electrotonus; its manner of folding together in response to stimulation is most decided; its endurance is considerable; and its sensitiveness to electrical stimuli is so great, that I have seen it respond to closure of the constant current supplied by a single DANIELL's cell when all the plugs of the rheochord were firmly pressed in, and the travelling mercury cups were only drawn out one quarter of an inch.

When, therefore, I began my investigation upon this animal, I thought that the

task of determining the questions before me would prove a comparatively easy one. Unfortunately my anticipations were not realized. The conducting-power of the gelatinous tissue (more or less of which is necessarily adherent to the marginal canal), the deleterious influence of the air upon the intrapolar portion of tissue which is necessarily exposed to it, the voluntary motions of the animal—these, and other elements of difficulty which I need not wait to specify, have proved so serious, that, although a great deal of labour has been expended upon this part of my subject, I do not yet feel myself justified in here giving a definite opinion with regard to it; and I have stated the foregoing details chiefly in the hope that the great importance of the inquiry may induce some other observer to assist me in conducting it. I may say, however, that I have obtained undoubted indications of a state of exalted sensibility in the extrapolar regions of the severed strip, although I am unable to say that I have obtained any satisfactory indications of a corresponding anelectrotonic state. I am not yet in a position to speak confidently with respect to PFLÜGER's law*.

(D) Before leaving the subject of electrical stimulation, there are still a few further observations to detail.

(α) The excitable tissues of Medusæ in their behaviour towards electrical stimulation conform in all respects to the rules which are followed by the excitable tissues of other animals. Thus closure of the constant current acts as a much stronger stimulus than does opening of the same, while the reverse is true of the induction-shock.

(β) As before stated, different species of Medusæ manifest different degrees of sensitiveness to electrical stimulation, though in all cases the degree of sensitiveness is wonderfully high.

(γ) When the constant current is passing in a portion of the strip of a severed margin, the nectocalyx sometimes manifests uneasy motions *during the time the current is passing*. It is possible, however, that these motions may be merely due to accidental variations in the intensity of the current.

(δ) When the intrapolar portion of the severed margin of *S. laciniata* happens to be *spontaneously* contracting prior to the passage of the constant current, the moment this current is thrown in these spontaneous contractions often cease, and are then seldom resumed until the current is again broken, when they are almost sure to recommence. This effect may be produced a great number of times in succession.

(ε) *Exhaustion* of the excitable tissue of the nectocalyx may be easily shown by the ordinary methods. Exhausted tissue is much less sensitive to stimulation than is fresh tissue. Moreover, so far as the eye can judge, the contraction is slower and the period of latent stimulation prolonged.

(ζ) It is important to observe that the *tetanus* produced by Faradaic electricity is not of the nature of an apparently single prolonged contraction (except, of course, such among the naked-eyed Medusæ as respond to all kinds of stimuli in this way), but

* I may here observe that it was in one of my numerous electrical experiments upon *Staurophora laciniata* that the exception to the fundamental experiment mentioned in Division II. was noticed.

that of a number of contractions rapidly succeeding one another—as in the heart under similar excitation. This apparent absence of summation will probably require further treatment on some future occasion.

(*g*) I shall now conclude my remarks on electrical stimulation by describing a highly remarkable phenomenon, and one which I am quite unable to explain. I am persuaded, however, that it is a phenomenon well meriting the attention of physiologists. When the swimming-bell of *Sarsia* has had its margin removed, and so, as proved by hundreds of similar experiments, has been entirely deprived of its locomotor centres, nevertheless in response to electrical stimulation, instead of giving a single contraction to make or break, it may begin a highly peculiar motion of a flurried, shivering character, which lasts without intermission for periods varying from a few seconds to half an hour. I never but once saw a similar motion in the perfect animal, and this was in the case of a specimen which was dying from having been poisoned with iron-rust. The motion, I think, may be explained by supposing that the various parts of the muscle-layer are contracting without coordination; but why they should sometimes do this in response to stimulation, and why, when they do this, they should continue the action so long—these questions I cannot answer. In the case of so peculiar a phenomenon, however, it is necessary that I should detail all the facts I have been able to collect. I have never seen any similar or corresponding action performed by the paralyzed bells of other Medusids, and even in the case of *Sarsia* its occurrence is comparatively rare. When it does occur, however, it is always continuous; that is to say, it never spontaneously recommences after having once ceased. As already stated, the period of its duration is extremely variable; but when this period is long, it is observable that the shivering motions become feebler and feebler, until they eventually fade away into quiescence. The animal is then quite dead to all further stimulation. Beyond saying that the peculiar motions in question never originate independently of stimulation, I cannot give much further account of the conditions which determine their commencement. The following instances are quoted from my notes *in extenso*:—

"A healthy individual with centres removed, after failing to respond to either make or break of direct current, and after about a quarter of a minute's rest from a series of rapidly alternating makes and breaks of this current, began to shiver, and continued to do so for five minutes. Afterwards quite dead."

"Another healthy individual, after refusing to contract either on make or break of induced current for two or three times, began to shiver and continued to do so for twenty minutes. Afterwards quite dead. This individual had been used five minutes before for experiments with the direct current, to which it responded well and without shivering."

"Another healthy individual was left for some time after excision of margin, and then put into the well and submitted to induction-shocks. No contraction either on make or break with coil pushed to zero. On now trying direct current, without altering position of electrodes, violent contraction on make and also a decided one on break.

On again trying induced current, no contraction. On again trying direct current, strong contractions [thus far, of course, the behaviour of the tissue was normal, see above § 2 (A)], and after four or five of these, shivering began; this lasted for four minutes, and, when again quiescent, the bell again responded to make and break of direct current in the ordinary way."

Now all that can be gathered from these and similar notes is, that the shivering motion in question may be started either by the direct or by the induced current, and this in some cases when the bell has repeatedly refused to answer stimuli in the ordinary way. It may further be gathered from these notes that shivering is most likely to begin after the bell has received a number of shocks in succession. I must also state that it is almost certain to ensue upon slightly acidulating the water in which the mutilated bell is suspended. The shivering, if it begins under these circumstances, will then continue for some time even after the bell is restored to normal sea-water.

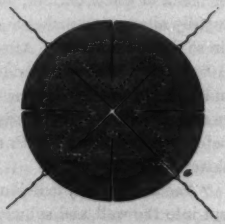
§ 3. *Chemical Stimulation.*—Under this heading I have very little to say, for the simple reason that the excitable tissues of Medusæ conform in every respect to the rules which are followed by the nervo-muscular tissues of higher animals. Both the severed locomotor centres and the mutilated swimming-organs, as well, I may add, as several polypites and tentacles, respond to applications of various acids, solutions of various metallic salts, alcohol, ether, glycerine, &c. It may here be stated that fresh water is quickly fatal to Medusæ, especially in the case of the naked-eyed group. This latter fact has been previously observed by Agassiz.

§ 4. *Thermal Stimulation.*—For the present I reserve my observations relating to this subject.

IV. Section.

§ 1. *Amount of section which the contractile tissues of Medusæ will endure without suffering loss of their physiological continuity.*—The extent to which the substance of the swimming-organs of Medusæ may be mutilated without undergoing destruction of their physiological continuity is in the highest degree astonishing. Again taking *Sarsia* as a type of the naked-eyed division, I shall here describe two modes of section which are the most trying that I was able to devise.

Fig. 2.



(*a*) Suppose the annexed diagram to represent *Sarsia* in projection, the lines being cuts. It will be seen that there are two systems of interdigitating cuts, with four radial cuts in each system. Those of the one system pass from the margin to two thirds of the way up the cone, while those of the other system pass in the form of a cross from the apex of the cone to two thirds of the way towards its base. It will thus be evident that a stimulus to contraction originating in any point *a* of the margin cannot radiate its influence throughout the whole contractile substance of the bell, except by traversing

the zigzag course of the dotted line. Yet in the case of healthy specimens the spontaneous contractions are apparently as synchronous over the entire extent of the nectocalyx as they are when this organ is in an unmutilated state. Further, if the extreme margin of the nectocalyx be now removed, the paralyzed organ will respond to stimuli applied at any point just as readily and as simultaneously over its whole extent as it would do were there no system of interdigitating cuts present.

(*b*) The other mode of section to which I have alluded is that of a simple spiral. If the margin of *Sarsia* be removed in the form of a continuous thread with one end attached to the nectocalyx (as already described in the case of *Staurophora laciniata*), and if the section be then continued in the form of a spiral having two or more turns from the base to the apex of the cone, a wave of contraction, starting from any point in the original margin of the animal, passes into the spiral upon reaching its point of origin, and then runs round and round the spiral from the base to the apex of the cone. In vigorous specimens the course of the contractile wave is so rapid that, in a spiral of one turn, it requires a quick eye to perceive its true nature: to most persons the contraction appears simultaneous over the entire spiral, whereas it is really a successive wave. But in the case of non-vigorous specimens, or of a spiral having two turns, even a slow eye may perceive the true nature of the contraction. Some specimens of *Sarsia* endure more turns of the spiral than do others; but in all cases the animal will live for a long time in this corkscrew-like shape, performing its spontaneous contractions as pertinaciously as ever. As might be expected from the analogy of the experiment last described, if the marginal centres be removed altogether, the paralyzed spiral will respond to the weakest stimulus applied at its lower end or any other part of its course, and this as vigorously as if no spiral section had been performed. I may here observe, in passing, that of all the experiments upon excitable tissues with which I am acquainted, there is no single instance of a series of contrasts so astounding as are those exhibited by *Sarsia*—first darting hither and thither with the greatest spontaneity and vigour, then reduced to a state of absolute quiescence by the removal of an intensely localized system of locomotor centres, but yet remaining so keenly sensitive to stimulation throughout its entire extent, as shown by the modes of section just described.

(*c*) The gonocalyces of the covered-eyed Medusæ, being of a much larger size than are the nectocalyces of the naked-eyed Medusæ, present much greater facilities for conducting experiments in section. Of the species of the covered-eyed Medusæ which I have had the opportunity of examining, *Aurelia aurita*, on account of its flat shape, is much the best suited for this line of inquiry. I have therefore made this species the subject of a very extensive investigation. Under the present heading, however, it will only be necessary for me to describe three observations.

As already stated, the concentration of locomotor centres into the lithocysts of this species is more marked than in the case of any other species I have met with, notwithstanding individual instances frequently occur in which feeble locomotor centres are also scattered through the general contractile tissue of the gonocalyx. It will happen, then,

that in any given case the chances are in favour of the individual experimented upon having most or all of its spontaneity aggregated, so to speak, in its eight lithocysts. If seven of these, therefore, be removed, all the spontaneous impulses to contraction must emanate from the remaining lithocyst. Indeed it may easily be seen that such is the case; for each pulsation of the gonocalyx is now of the nature of a double wave of contraction —the two waves starting simultaneously from the remaining lithocyst, each to run rapidly and equally in opposite directions, and so to meet at the point of the gonocalyx that is opposite to the lithocyst. Well, if this remaining lithocyst be made the point of origin of a spiral section which is carried round and round the flat-shaped disk, the result of course is a long strip of tissue, terminating at one end in the lithocyst, and at the other end in the remainder of the gonocalyx (see Plate 33*). A contractile wave proceeding from the lithocyst has now either to become blocked at some point in the length of the strip, or to traverse the whole length of the strip and deliver itself into the remaining contractile tissue of the gonocalyx. The conditions which determine the blocking of a contractile wave under these circumstances will be fully treated of further on: meanwhile it is enough to say that, as might be expected, the length and width of the strip are very important factors, but that, nevertheless, there are immense individual differences in the endurance of the contractile tissue under this form of section. The highest degree of such endurance that I have met with has been two and a half turns of the spiral (see Plate 33). The strip in this case was about an inch wide and nearly a yard long. I doubt not, however, that a wonder-seeker, by making a sufficient number of such experiments, could obtain results even more surprising.

(*d*) The second observation will be best appreciated by a glance at the accompanying woodcut (fig. 3), which is a drawing made from life of an individual submitted to radial

Fig. 3.

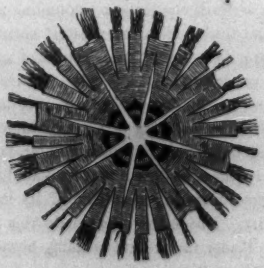


Fig. 4.

section in the way represented. The contractions emanating from the remaining lithocyst (*l*) passed through the entire gonocalyx with no appreciable diminution of vigor, so that I would have increased the severity of the section but for want of space.

* The central organs in this and in the preceding Plate are partly copied from Prof. L. Agassiz's representation of an allied species, and so are not perfectly accurate.

(*e*) The third observation will be readily understood from the annexed diagrammatic representation of *Aurelia aurita* (fig. 4). The central circle (*x*) stands for an open space cut out of the gonocalyx; the outer circle indicates the margin of the animal, with all lithocysts save one (*l*) removed; and the median circular line represents a cut. It will be seen that the effect of this cut is almost completely to sever the mass of tissue (*y z*) from the rest of the gonocalyx, the only connexion between them being the narrow neck of tissue at *y*. Yet, in the case to which I refer, the contractile waves emanating from *l* passed in the directions represented by the arrows without undergoing any appreciable loss of vigour. Upon completing the circular cut at *y*, the ring of tissue (*y z*) became totally paralyzed, while the outer circle of course continued its contractions as before. Now the neck of tissue at *y* measured only $\frac{1}{8}$ inch across, while the ring of tissue *y z* when cut through and straightened out upon the table measured 1 inch across and 16 inches in length. That is to say, 16 square inches of tissue derived its impulse to vigorous contraction through a channel $\frac{1}{8}$ inch wide, notwithstanding the latter was situated at the furthest point of the circle from the discharging lithocyst which the form of the section rendered possible. It should be stated, however, that this experiment might be repeated a number of times without yielding a similar result. I regret that in this instance I did not try the effect of narrowing this neck of tissue still more; for, from the analogy afforded by numberless observations, I entertain but little doubt that some portion of this neck of tissue was pervaded by a very slender though very definite line of functionally differentiated tissue; and that if this line of differentiated tissue had not happened to be cut through in the narrowing of the connecting isthmus, the width of the latter might have been reduced to a half, a quarter, or even less, without impeding the passage of the contractile wave.

§ 2. (*a*) *Nature of the contractile tissues of swimming-organs.*—The last assertion leads us to this important part of our subject. Under this heading I propose to treat of the question, What is the nature of the general contractile substance of Medusæ? Is the contractile tissue of the swimming-organ pervaded by a definite system of sensory and motor tracts, so to speak, radiating respectively to and from the marginal centres? or is the contractile tissue of the swimming-organ of a more primitive nature, the functions of nerve and muscle being more or less blended throughout its substance? Now, for my own part, I deem this question the most interesting one with which the present paper is concerned; for the evolutionist, no less than the physiologist, will recognize its importance as of the highest. We have already obtained ample evidence of the fact that it is to the Medusæ we must look for the first decided integrations of tissue having, to say the least, something closely resembling a nervous function to subserve; and we have seen that these integrations appear in the form of intensely localized centres of spontaneity. It therefore becomes a matter of pressing moment to ascertain the manner in which the spontaneous impulses are transmitted from these centres and distributed throughout the contractile tissue of the swimming-organ—whether a definite system of lines of discharge becomes evolved *pari passu* with a defi-

nite system of centres of spontaneity, or contractile tissue can afford, so to speak, to retain more or less of its protoplasmic nature after spontaneity has become so far developed as to be localized in definite centres. In treating of this question, I will only resort to theory when compelled to do so by the facts.

From the observations already detailed it might well be concluded that the method of inquiry by section has already settled the question before us, seeing that this method has apparently reduced the hypothesis as to the presence of definite lines of discharge to an absurdity. A moment's thought will render obvious how very trying the spiral form of section already described (Plate 33) must be to any thing resembling a nervous plexus, while a glance at fig. 3 would seem to render the supposition as to the presence of any such plexus almost impossible. Nevertheless there is a weighty body of evidence to be adduced on the other side.

(*b*) Confining our attention to the species which, as already observed, is in every respect the best suited for sectional experiments, viz. *Aurelia aurita*, it is to be observed, in the first place, that it is the exception and not the rule for specimens to stand the spiral mode of section more than once round the swimming-organ without losing the physiological continuity of their tissues. Moreover different specimens exhibit extreme variations in their tolerance of this mode of section. Sometimes the contractile wave will become blocked when the contractile strip is only an inch long, while in other cases, as already stated, the wave will continue to pass through a strip more than thirty times that length; and between these two extremes there are all possible grades of tolerance. Now it seems to me that if the tissue through which these contractile waves pass is supposed to be of a functionally homogeneous nature, no reason can be assigned why there should be such great differences in the endurance of different individuals of the same species; while if we suppose that the passage of these contractile waves is more or less dependent on the presence of more or less differentiated lines of discharge, we encounter no difficulty; for it is almost to be expected that in such lowly forms of life such lines of discharge, if present, should not be constant as to position. In some cases, therefore, it would happen that important lines of discharge would soon be encountered by the section, while in other cases it would happen that such lines of discharge would escape the section for a longer distance. It is, indeed, almost incredible that any one line of discharge should happen to pursue a spiral course twice or thrice round the animal, and at the same time happen to be concentric with the course pursued by the section; but such an hypothesis is not necessary to account for the facts. All we have to assume is that there exists *a more or less intimate plexus* of such lines of discharge, the constituent elements of which are endowed with the capacity of vicarious action, and that in some cases the section happens to leave a series of their anastomoses in a continuous state. Doubtless even this assumption represents a state of things very difficult to believe; but I do not see that the numberless grades of individual variations already mentioned admit of being accounted for in any other way. Moreover I think that the difficulty of accepting this explanation will diminish if we cease

to regard the hypothetical plexus as presenting the high degree of integration characteristic of a properly nervous plexus; but in this preliminary paper I cannot, without undue length, discuss this subject.

(*c*) The strongest evidence of definite lines of discharge being present, however, is yet to be adduced; and this consists in the following invariable fact:—*At whatever point in a strip that is being progressively elongated by section the contractile wave becomes blocked, the blocking is sure to take place* completely *and* exclusively *at that point.* Whereas up to the time that the incision reached quite up to that point the contractile waves showed no signs of meeting with any resistance in their passage from the severed strip to the rest of the gonocalyx, immediately after the incision is carried through that point the blocking of the contractile waves is total. Now, as I have tried this experiment a great number of times, and always tried it by carefully feeling the way round (*i. e.* only making a very short continuation of the cut after the occurrence of each contractile wave, and so very precisely localizing the spot at which the contractile waves ceased to pass into the gonocalyx), I can scarcely doubt that in every case the blocking is caused by cutting through a very slender line of tissue which was in some way or other differentiated from the surrounding tissue, and which, in virtue of its differentiation, had previously served to convey the contractile influence from the strip to the remainder of the gonocalyx. Why it should sometimes be so long before such slender lines of tissue are encountered by the section, or *a sufficient number* of them encountered to destroy the physiological continuity of the tissue, may well afford matter for surprise; but I must nevertheless assert my persuasion that, so far as my observations have yet gone, a legitimate deduction from them appears to be, that in every individual of this species (and so from analogy, as well as observations on other species, probably in all the Medusæ) these slender lines of differentiated tissue are present, that through their mediation the spontaneous impulses originating in the marginal centres are communicated to the contractile tissue of the swimming-organ, and therefore that these slender lines of differentiated tissue are functionally, if not structurally, nerves.

Although I intend for the present to reserve my observations on the histological part of the inquiry, I may here state, in passing, that I have hitherto failed to distinguish any structural modification of the tissue in the regions occupied by these supposed lines of discharge. On one occasion, when I made the radial incision on one side of the single remaining lithocyst, preparatory to making the circumferential incision necessary to procure a contractile strip, I was surprised to find that the entire gonocalyx, although previously contracting with vigour, became wholly paralyzed. Now the incision which I made was only half an inch long, and the effect it produced was amply sufficient to prove that the influence of the lithocyst had previously been communicated to the gonocalyx *from one side only*. I therefore concluded that somewhere within the small band of tissue half an inch long and quarter of an inch broad, which was included between the incision and the lithocyst, there must have been a line of discharge of sufficient size to convey the influence of the lithocyst to the entire gonocalyx. Yet

upon staining this small portion of tissue with chloride of gold, I was unable to perceive any structural peculiarity that might be supposed to correspond with the functional peculiarity which it had previously exhibited.

(*d*) I have now to detail another fact of a very puzzling nature, but one which is certainly of great importance in its bearing upon the subject of the present section. When the spiral section is performed on *Aurelia aurita*, and when, as a consequence, the contractile waves which traverse the elongating strip become at some point suddenly blocked, if the section be stopped at this point it not unfrequently happens that after a time the blocking suddenly ceases, the contractile waves again passing from the strip into the gonocalyx as freely as they did before the section reached the point at which the blocking occurred. The time required for this restoration of physiological continuity is very variable, the limits being from a few seconds to an hour or more. Usually, however, the time required is from two to four minutes. This process of reestablishing the physiological connexions, although rapid, is not so instantaneous as is that of their destruction by section. In general it requires the passage of several contractile waves before the barrier to the passage of succeeding waves is completely thrown down. The first wave which effects a passage appears to have nearly all its force expended in overcoming the barrier, the residue being only sufficient to cause a very feeble, and sometimes almost imperceptible, contraction of the gonocalyx. The next wave, however, passes across the barrier with more facility, so that the resulting contraction of the gonocalyx is more decided. The third wave, again, causes a still more pronounced contraction of the gonocalyx; and so on with all succeeding waves, until every trace of the previous blocking has disappeared. When this is the case it generally happens that the strip will again admit of being elongated for a short distance before a blocking of the contractile wave again supervenes. Sometimes it will be found that this second blockage will also be overcome, and that the strip will then admit of being still further elongated without the passage of the waves being obstructed; and so on occasionally for three or four stages.

The same series of phenomena may be shown in another way. If a contractile strip of tolerable length be obtained with the waves passing freely from one end to the other, and if a series of parallel and equidistant cuts be made along one side of the strip, in a direction at right angles to the length and each cut extending across two thirds of the breadth of the strip, the chances are in favour of the contractile waves being wholly unaffected by the sections, however numerous these may be. But now, if another series of parallel and equidistant cuts of the same length as the first ones, and alternating with them, be made along the other side of the contractile strip, the result is, of course, a number of interdigitating cuts; and it is easy to see that by beginning with a few such cuts and progressively increasing their number, a point must somewhere be reached at which one portion of the strip will become physiologically separated from the rest. The amount of such section, however, which contractile strips will sometimes endure is truly surprising. I have seen such a strip 20 inches long by 1½ inch wide, with ten such cuts

along each side, and the contractile waves passing without impediment from end to end. But what I wish more especially to observe just now is, that by progressively increasing the number of such interdigitating cuts up to the point at which the contractile wave is blocked and then leaving the tissue to recover itself, in many cases it will be observed that the blocking is sooner or later overcome, that on then adding more interdigitating cuts the blocking again supervenes, but that in time it may again be overcome, and so on. It is, however, comparatively rare to find cases in which blocking is overcome twice or thrice in succession.

(*e*) Section is not the only way in which blocking of waves may be caused in contractile strips. I find that pressure, even though very gentle, exerted on any part of a strip causes a blocking of the waves at that part, even after the pressure has been removed. If the pressure has been long continued, after its removal the blocking will probably be permanent; but if the pressure has been only of short duration, the blocking will most likely be transitory. Even the slight strains caused by handling a contractile strip in the air are generally followed by a decrease in the rate of the waves, and sometimes by their being completely blocked. Other methods by which the passage of waves in contractile strips admits of being blocked will be alluded to further on.

(*f*) Such are some of the facts I have been able to collect bearing on the question concerning the physiological character of the general contractile tissues of the Medusæ. That these facts are of a somewhat paradoxical nature is evident; and whether or not there is any theory by which they admit of being satisfactorily reconciled is doubtful. I may say, however, that I think there is such a theory, and that I only refrain from publishing it at the present time because I think that at this early stage of the inquiry it is desirable, as much as possible, to avoid speculation.

V. Additional facts tending to prove the identity of the specialized marginal tissue of Medusæ with nervous tissue in general.

§ 1. *Sense-organs.*—It has long been thought more or less probable that the so-called "eye-specks" of Medusæ are rudimentary or incipient organs of vision; but I am not aware that any one has hitherto endeavoured to test the supposed probability by experiment. I say "supposed probability," because, in the absence of any structural resemblance to an ocellus, I do not see how speculation as to the function of these organs can be of any further value than a guess*. The guess, however, in this case happens to be correct.

* [Postscript II.—It is with considerable pleasure that I am now able to add the following very judicious and philosophical confirmation of this opinion by so high an authority as Prof. Haeckel:—"Die Deutung der Sinnesorgane niederer Thiere gehört ohne Zweifel zu den schwierigsten Objecten der vergleichenden Physiologie und ist der grössten Unsicherheit unterworfen. Wir sind gewohnt, die von den Wirbelthieren gewonnenen Anschauungen ohne Weiteres auch auf die wirbellosen Thiere der verschiedenen Kreise zu übertragen und bei diesen analoge Sinnesempfindungen anzunehmen, als wir selbst besitzen." Prof. Haeckel, indeed, inclines to the belief that the marginal vesicles which he examined are sense-organs of some kind; but this is a very different position

Having put two or three hundred *Sarsiæ* into a large bell-jar, I completely shut out the daylight from the room in which the jar was placed. By means of a dark lantern and a concentrating lens, I then cast a beam of light through the water in which the *Sarsiæ* were swimming. The effect upon the latter was most decided. From all parts of the bell-jar they crowded into the path of the beam, and were most numerous at that side of the jar which was nearest to the light. Indeed close against the glass they formed an almost solid mass, which followed the light wherever it was moved. The individuals composing this mass dashed themselves against the glass nearest the light with a vigour and determination closely resembling the behaviour of moths under similar circumstances. There can thus be no doubt about *Sarsia* possessing a visual sense.

The method of ascertaining whether this sense is lodged in the eye-specks was, of course, extremely simple. Choosing a dozen of the most vigorous specimens, I removed all the eye-specks from nine, and placed these together with the three unmutilated ones in another bell-jar. After a few minutes the mutilated animals recovered from their nervous shock, and began to swim about with tolerable vigour. I now darkened the room, and threw the concentrated beam of light into the water as before. The difference in the behaviour of the mutilated and of the unmutilated specimens was very

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to have occupied with regard to this matter from that which ventured upon bold assertions as to the specific function of these organs. Now, forasmuch as the above paragraph in the text was written without reference to Prof. Haeckel's work, I should here like to add the remark that, in my opinion, his deductions concerning this matter differ from those of previous writers in the important particular that they were warranted by the facts of structure which he observed. Granting that he had satisfied himself as to the nervous character of the tissue he describes, and the peculiarly significant distribution of this tissue in the marginal vesicles which he figures appears to me certainly to justify his conclusion that "was die Deutung der Randkörperchen nach Feststellung dieses complicirteren Baues anlangt, so wird zunächst ihre allgemein gültige Stellung als *Sinnesorgane* dadurch nur befestigt." And it is of course needless to say that with the next succeeding sentences I fully concur. "Was aber die speciellere Feststellung der Sinnesqualität betrifft, so scheint mir diese dadurch nach keiner Richtung hin bestimmter bezeichnet zu werden. Im Gegentheil glaube ich, dass damit nur die wesentliche Differenz dieser Randbläschen von anderen ähnlichen Sinnesorganen niederer Thiere, z. B. von den meist zunächst damit verglichenen Gehörbläschen der Würmer und Mollusken, noch mehr bestätigt und ausdrücklich hervorgehoben wird. . . . . Noch weniger freilich als die von den meisten Autoren angenommene Deutung der Randbläschen unserer Medusen als Gehörorgane kann die von Agassiz und Fritz Müller vertretene Ansicht befriedigen, dass dieselben Augen seien. . . . . Alle diese Verhältnisse sind mit der Deutung der Concretion als 'Linse' und des sie umschliessenden Sinnesganglion als 'Sehnerv' durchaus unvereinbar."

It may not be unnecessary to say that, although the simple experiment above described effectually proves that the marginal bodies have a visual function to subserve, we are not for this reason justified in concluding that these bodies are so far specialized as organs of sight as to be precluded from ministering to any other sense. Therefore the results of the above-mentioned experiments cannot be held in any way to affect the judgment of Prof. Haeckel:—"Und doch ist es viel wahrscheinlicher, dass hier wesentlich andere Sinnesempfindungen zu Stande kommen, von deren eigentlicher Qualität wir uns keine bestimmte Vorstellung machen können; wie es z. B. sehr wahrscheinlich ist, dass die Empfindung der Licht- und Schallwellen, für welche bei den höheren Thieren verschiedene Organe differenzirt sind, bei den niederen an ein und dasselbe Sinnesorgan, natürlich in unvollkommener Ausbildung, gebunden vorkommen." (For the quotations *vide loc. cit.* pp. 57, 58.)—Feb. 1876.

marked. The three individuals which still had their eye-specks sought the light as before, while the nine without their eye-specks swam hither and thither without paying it any regard.

A further question, however, still remained to be determined. The pigment-spot of the eye-speck in Medusæ is, as Agassiz observes, placed *in front of* the presumably nervous tissue; and for this reason he naturally enough suggests that if the eye-speck has a visual function to perform, the probability is that the rays by which the organ is affected are the heat-rays lying beyond the range of the visible spectrum. Accordingly I brought a heated iron just ceasing to be red close against the large bell-jar which contained the numerous specimens of *Sarsia*; but not one of the latter approached the heated metal.

From these observations, therefore, I conclude that in *Sarsia* the faculty of appreciating luminous rays is present, and that this faculty is lodged exclusively in the eye-specks. My observations on the other genera of Medusæ in this connexion are not yet complete.

§ 2. *Effects of various Poisons on the Locomotor System of Medusæ.*—As this communication has now grown to an undue length, I shall reserve for a future paper many facts of great physiological interest regarding luminosity, general distribution of the supposed lines of discharge, coordination of the centres of spontaneity, rate of transmission of contractile waves in different genera and under various forms of section, &c., and shall conclude what I have to say at the present time by describing the effects of a few among the poisons I have tried upon the Medusæ, choosing those upon the list which most tend to prove the identity of the specialized marginal tissue of these animals with nervous tissue in general.

(*a*) The anæsthesiating influence of chloroform and ether is most decided. This fact, I find, has also been observed by Agassiz; and he remarks in effect that even if it stood alone it ought to be considered sufficient to demonstrate the presence of nerves in Medusæ. Without straining our deductive powers quite so far as this, I think that the marked influence of chloroform and ether upon the Medusæ may properly be taken as in some measure confirmatory of the doctrine which that great naturalist so strenuously upheld.

Agassiz appears to have tried the effect of chloroform only in the case of *Sarsia*. I may therefore state that in all the other genera I have experimented upon, both of the naked- and covered-eyed groups, the anæsthesiating influence of this substance is equally decided. This influence, moreover, is in every respect precisely similar to that which is observable in the case of the higher animals. Soon after a few drops of chloroform have been added to the water in which a vigorous medusid is contained, the locomotor pulsations of the latter become slower and slower in the time occupied by their execution, while the intervals of diastole become more and more prolonged. Concurrently with this slowing of the pulsations their strength naturally grows less and less vigorous, so that eventually the systoles are separated from one another by five or six times the

normal interval, and when they occur are of the feeblest character. Soon after this stage has been reached the systoles altogether cease; and in a few seconds after they have done so the animal fails to respond even to the strongest stimuli; and this, be it remembered, is quite as remarkable a fact in the case of Medusæ as it is in the case of the higher animals. The time occupied by the whole of this process varies with different species; but it is always very brief, namely (speaking from memory) about fifteen seconds to a minute in the case of *Sarsia* and eighty seconds to two minutes in that of *Aurelia aurita*. But brief as is the time required for chloroform to assert its influence upon Medusæ, it is long as compared with the time required for its effects to pass off when the animal is again restored to normal sea-water. A specimen of *Sarsia* which has been completely anæsthesiated, and so to all appearance perfectly dead, resumes its pulsations a few seconds after being again immersed in unpoisoned water. There appears to be a relationship, however, between the time required for complete anæsthesiation and that required for complete subsequent recovery, for the recovery of *Aurelia aurita* takes a few seconds longer than does that of *Sarsia*. In all cases the recovery is progressive, the first pulsations being very feeble and the periods of diastole prolonged; but very shortly the pulsations resume their normal strength and frequency. The same animal may then, of course, be subjected to a repetition of the experiment, and this for an indefinite number of times.

(*b*) The anæsthesiating effects of morphia are as decided as are those of chloroform. I shall confine myself to describing the process of anæsthesiation in the case of *Aurelia aurita* in an extract from my notes:—"A very vigorous specimen, having twelve lithocysts, was placed in a somewhat strong sea-water solution of morphia. Half a minute after being introduced commencement of torpidity ensued, shown by contractions becoming fewer and feebler. In one minute the feeble impulses emanating from the prepotent lithocyst failed to spread far through the contractile tissue, appearing to encounter a growing resistance. Eventually this resistance became so great that only a very small portion of contractile tissue in the immediate neighbourhood of the lithocyst contracted, and this in a very slow and feeble way. Two minutes after immersion even these partial contractions entirely ceased, and soon afterwards all parts of the animal were completely dead to stimulation. Recovery in normal water slower than that after chloroform, but still soon quite complete. Repeated experiment on this individual four times without injury."

(*c*) The species I shall choose for describing the effects of strychnia is *Cyanæa capillata*, which is most admirably adapted for experiments with this and some of the other alkaloid poisons, from the fact that, in water kept at a constant temperature, its pulsations are as regular as are those of a heart. After *Cyanæa capillata* has been allowed to soak for ten minutes or so in a weak sea-water solution of strychnia, unmistakable signs of irregularity in the pulsations supervene. This irregularity then increases more and more, till at length it grows into well-marked convulsions. The convulsions manifest themselves in the form of extreme deviations from the rhythmical contractions

so characteristic of *Cyanœa capillata*. Instead of the heart-like regularity with which systole and diastole follow one another in the unpoisoned animal, we now have periods of violent and prolonged systole resembling tonic spasm; and when the severity of this spasm is for a moment abated, it is generally renewed before the gonocalyx has had time again to become fully expanded. Moreover the spasm itself is not of uniform intensity throughout the time it lasts; but while the gonocalyx is in a continuously contracted state, there are observable a perpetual succession of extremely irregular oscillations in the strength of the contractile influence. It is further a highly interesting fact that the convulsions are very plainly of a *paroxysmal* nature. After the gonocalyx has suffered a prolonged period of convulsive movements, it expands to its full dimensions, and in this form remains for some time in a state of absolute quiescence. Presently, however, another paroxysm supervenes, to be followed by another period of quiescence, and so on for hours. The periods of quiescence are usually shorter than are those of convulsion; for while the former seldom last more than forty seconds or so, the latter may continue uninterruptedly for five or six minutes. In short, Medusæ, when submitted to the influence of strychnia, exhibit all the symptoms of strychnia poisoning in the higher animals. Death, however, is always in the fully expanded form.

(*d*) Curare has already been tried upon Medusæ, and is stated to have produced no effects; it is therefore especially desirable that I should first of all describe the method of exhibiting it which I employed.

Having placed the medusid to be examined in a flat-shaped beaker, I filled the latter to overflowing with sea-water. I next placed the beaker in a large basin, into which I then poured sea-water until the level was the same inside and outside the beaker, *i. e.* until the two bodies of water all but met over the brim. Having divided the medusid across its whole diameter, with the exception of a small piece of marginal tissue at one side to act as a connecting-link between the two resulting halves, I transferred one of these halves to the water in the basin, leaving the other half still in the beaker, the marginal tissue which served to unite the two halves being thus supported by the rim of the beaker. Over the minute portion of the marginal tissue which was thus of necessity exposed to the air, I placed a piece of blotting-paper which dipped freely into the sea-water. Lastly, I poisoned the water in the beaker with successive doses of curare solution.

The results obtained by this method were most marked and beautiful. Previous to the administration of the poison both halves of the medusid were of course contracting vigorously, waves of contractile influence now running from the half in the beaker to the half in the basin, and now *vice versâ*. But after the half in the beaker had become effectually poisoned by the curare, all motion in it completely ceased, the other, or unpoisoned half continuing to contract independently. I now stimulated the poisoned half by nipping a portion of its margin with the forceps. Nothing could be more decided than the result. It will be remembered that when any part of *Staurophora laciniata* is pinched with the forceps or otherwise irritated, the motion of the whole

body which ensues is totally different from that of an ordinary locomotor contraction, all parts folding together in one very strong and long-protracted systole, after which the diastole is very much slower than usual. Well, on nipping any portion of the poisoned half of *Staurophora laciniata*, this half remained absolutely motionless, while the unpoisoned half, though far away from the seat of irritation, immediately ceased its normal contractions, and folded itself together in the very peculiar and distinctive manner just described. This observation was repeated a number of times, and, when once the requisite strength of the curare solution had been obtained, always with the same result. The most suitable strength I found to be 1 in 2500, in which solution the poisoned half required to soak for half an hour.

I also tried the effect of this poison on the covered-eyed Medusæ, and have fairly well satisfied myself that its peculiar influence is likewise observable in the case of this group.

It has further to be stated that when the poisoned half is again restored to normal sea-water, the effects of curare pass off with the same astonishing rapidity as is observable in the case of the other poisons which I have tried. Thus, although an exposure of half an hour to the influence of curare of the strength named is requisite to destroy the motor power in the case of *Staurophora laciniata*, half a minute is sufficient to ensure its incipient return when the animal is again immersed in unpoisoned water.

It is also to be observed that a very slight degree of *over*-poisoning paralyzes the transmitting system as well as the responding one; so that if any one should repeat my observation, I must warn him against drawing erroneous conclusions from this fact. Let him use weak solutions with prolonged soaking, and by watching when the voluntary motions in the poisoned half first cease, he need experience no difficulty in obtaining results as decided as it is possible for him to desire.

I think it would be difficult to overrate the importance of these results: to my mind they are perhaps the most interesting which are contained in this paper. They not only prove that curare poison is consistent in manifesting its remarkable property when applied to these the lowest forms of life that present the beginnings of a nervous system; but they prove what is far more important, that in animals which, as we have seen from other evidence, present us with the first indications of a nervous system, the latter appears to have already undergone a differentiation in its functions, such that it is capable not only of influencing contiguous contractile parts, but also of being influenced by distant excitable parts.

(*e*) I shall conclude all I have to say at the present time upon the subject of poisons by stating the interesting fact, that if any of the narcotic or anæsthesiating agents be administered to any portion of a contractile strip cut from the gonocalyx of *Aurelia aurita* in the way already described, the rate of the contractile waves is at first progressively slowed (I shall give the actual tracings in a future paper), and eventually their passage is completely blocked at the line where the poisoned water begins. Upon now restoring the poisoned portion of the contractile strip to normal

sea-water the blocking is gradually overcome, and eventually every trace of it disappears. This experiment was suggested to me by Dr. BURDON SANDERSON*.

The contractile wave may be blocked by poisons in another way. A glance at Plate 33 will show that a circumferential strip cut from the gonocalyx of *Aurelia aurita* is pervaded transversely by a number of nutrient tubes, which have all been cut through by the section. At the side of the strip, therefore, furthest from the margin there are situated a number of open ends of these nutrient tubes. Now on injecting any of the narcotic poisons into one of these open ends, the fluid of course permeates the whole tube, and the contractile wave becomes blocked at the transverse line occupied by the tube as effectually as if the contractile strip had been cut through at that line.

A glance at Plate 32, again, will show that each lithocyst is surrounded by one of these nutrient canals. Upon injecting this canal, therefore, in a contractile strip, the effect of the poison may be exerted on the lithocyst more specially than it could be by any other method of administration. In view of recent observations concerning the effects of curare on the central nervous masses of higher animals, it may be worth while to state that a discharging lithocyst of *Aurelia aurita*, when thus injected with curare, speedily ceases its discharges. This fact alone, however, would not warrant any very trustworthy conclusions as to the influence of curare upon discharging centres; for it is within the limits of possibility that the paralyzing effects may here be due to the influence of the poison on the surrounding contractile tissue.

It is interesting to observe that if the discharging lithocyst be injected with chloroform, or a not too strong solution of morphia, it recovers in the course of a night, while with alcohol the first effects of the injection are considerably to accelerate the frequency and to augment the potency of the discharges; but the subsequent effects are a gradual diminution in the frequency and the vigour of these discharges until eventually total quiescence supervenes. In the course of a few hours, however, the torpidity wears away, and finally the medusid returns to its normal state.

VI. GENERAL SUMMARY.

There is very good analogical reason to expect that, in the case of the naked-eyed Medusæ, the exclusive localization of centres of spontaneity in the margins of nectocalyces will be found to be a very general, if not a constant, feature in the anatomy of the entire group. In six of the most divergent genera that occur in this group I have found it to be almost uniformly true that excision of the entire periphery of a nectocalyx is

* In conducting this experiment care must be taken not to exert the slightest pressure on any part of the strip (see IV. § 2 (*e*) p. 295). The method I adopted, therefore, was to have a vessel with a very deep furrow on each of its opposite lips. Upon filling this vessel to the level of these furrows with the poisoned water, and then immersing the whole vessel in ordinary sea-water up to the level of its brim, some of the poisoned water of course passed through the open furrows. The external body of water (*i. e.* the normal sea-water containing the animal) was therefore made proportionally very large, so that the slight escape of poison into it did not affect the experiment. On now passing the portion of the strip to be poisoned through the two opposite furrows it was allowed to soak in the poison while freely floating, and so without suffering pressure in any of its parts.

invariably followed by immediate, total, and permanent paralysis of the entire structure. I say *almost uniformly true*, for it will be remembered that in one individual instance three distinct centres of spontaneity remained after removal of all the marginal tissue. This individual instance occurred in a medusid belonging to the species *Staurophora laciniata*; and as this is the species which I found best suited for my experiments in electrotonus, I have had occasion to remove the marginal tissue from many scores of individuals belonging to it, and have never met with any but this one exception to a rule shown to be general by hundreds of experiments on the thirteen species named.

With the covered-eyed Medusæ the case is not so definite; for although centres of spontaneity unquestionably occur in the margins of all the members of this group which I have examined, these are not always, nor even generally, the only centres present. Looking to the order as a whole, so far as my experience extends, it is the exception and not the rule to obtain complete and permanent paralysis by excision of the marginal tissue of individuals composing this group. Considerable differences, however, are manifested by different species in this respect.

In *Sarsia* I find that a higher degree of paralyzing effect is produced by cutting out the four eye-specks alone than is produced by cutting out the intertentacular tissue alone; and I therefore conclude that the eye-specks are the principal seats of spontaneity. But they are far from being the *only* seats of spontaneity; for even the smallest atom of intertentacular tissue is sufficient, in the case of vigorous specimens, to animate the entire nectocalyx.

In none of the covered-eyed Medusæ examined have I found any evidence of the marginal tissue between the lithocysts being endowed with spontaneity. On the contrary, in the case of *Aurelia aurita*, which from its flat shape admits of fairer experimentation in this connexion than do any of the other genera examined, it is quite certain that all the spontaneity of the margin, and so, in most cases, of the whole animal, is concentrated in the eight lithocysts.

All Medusæ, after being paralyzed by the loss of their marginal centres, respond to all kinds of stimulation, and this by performing whatever action they would have performed in response to the stimulation employed had they been in their perfect state. Different species, however, manifest different degrees of irritability in their behaviour towards stimulation, although in all cases the degree of irritability is high.

Regarding electrical stimulation, both severed margins and the swimming-organs from which they have been taken are responsive both to the constant and to the induced current; but while severed margins remain responsive to weak induction-shocks after they cease to be affected by make and break of strong constant currents, the reverse is true of the mutilated swimming-organs; for, in the case of *Sarsia*, these remain responsive to make and break of the constant current even after they cease to respond to Faradaic electricity with the secondary coil pushed to zero (one cell).

The presence of excitable tracts has been proved in the case of *Sarsia* by means of electrical stimulation. The results are, that there is a progressive increase of excitability

from the apex to the base of the nectocalyx, that the excitability is greater in the regions of the eye-specks than anywhere else in the course of the circular canal, and that it is greatest of all in the vesicular part of an eye-speck. Further, the radial canals present a higher degree of irritability than does the intermediate tissue.

A mode of section, which I need not again describe, renders it possible to experiment with the view of ascertaining whether or not the specialized marginal tissue of the Medusæ shows any indications of polarity while under the influence of the constant current. The inquiry, however, is attended with serious difficulties; so that at present I am only able to say that although I have sometimes obtained satisfactory indications of kathelectrotonus, I have never obtained the slightest indications of anelectrotonus. With respect to PFLÜGER's law, notwithstanding I have spent a great deal of time over the subject, the evidence is too contradictory to be depended upon.

The contractile tissues of the Medusæ, in the comparative irritability they manifest towards make and break, upon the whole conform to the rules which are followed by irritable tissues in general.

The constant current during the time it is passing through a portion of the marginal tissue appears to have the power of inhibiting the spontaneous impulses to contraction which were previously originating in that portion; for so long as the current continues to pass, such spontaneous impulses sometimes cease in the intrapolar portion of the marginal tissue, and are renewed as soon as the current is broken.

Exhaustion of the contractile tissue may be easily shown by the ordinary methods, and in exhausted tissue, so far as the eye can judge, the contractions are slower and the period of latent stimulation prolonged.

The tetanus which is caused by Faradaic electricity is of the nature of a number of contractions following one another in quick succession with perceptible intervals between them.

Mutilated *Sarsiæ*, when stimulated by electricity or acidulated water, sometimes exhibit a highly peculiar and anomalous movement; but it is unnecessary to enter into all the details a second time.

With regard to chemical stimulation there is not much to say; for in none of the excitable tissues of the Medusæ have I found any exception to any of the rules which are conformed to by the excitable tissues of other animals.

My observations on the behaviour of the Medusæ in relation to thermal influences are omitted from the present paper.

Concerning the physiological properties of the general contractile tissue of swimming-organs, I confine myself in this paper to stating the results obtained by the spiral mode of section figured on Plate 33. These results are as follow. Different individuals of the species *Aurelia aurita* manifest great variations in the amount of spiral section they endure before the contractile strip becomes physiologically separated from the rest of the gonocalyx. In the majority of cases the contractile strip becomes physiologically separated from the rest of the gonocalyx before the spiral section has passed

once round the latter. It is comparatively rare to find cases in which contractile waves continue to pass after the spiral incision has been carried twice round this organ; and it is still more rare to find cases of waves passing in specimens such as that represented in Plate 33, where the spiral section has made two and a half turns round the gonocalyx. When such cases as the latter do occur, if the specimen happens to be an ordinary-sized one, the contractile strip will be about a yard in length. On the other hand, cases may occur in which blocking of the contractile wave supervenes when the contractile strip is only an inch long; and in one case complete blocking of this wave was caused by the *radial* incision half an inch long, made on one side of a freely discharging lithocyst, *i. e.* before the *circumferential* incision was begun at all. But such extreme variations upon the side of intolerance of spiral section are as uncommon as are the extreme variations upon the side of tolerance. Now the fact that between these two extremes there are to be found all possible grades of tolerance, appears to warrant us in concluding that the contractile tissue of *Aurelia aurita* is not of a functionally homogeneous nature.

And this conclusion is very much strengthened by the additional fact that at whatever point in a contractile strip which is being progressively elongated by section the contractile wave becomes blocked, the blocking is sure to take place completely and exclusively at that point. This fact, it appears to me, can only be properly explained by supposing that more or less differentiated lines of discharge pervade the contractile tissue of the gonocalyx, and that the sudden and complete blocking of the contractile waves which invariably takes place at some determinate point during the progress of the section is due to the latter having at that point severed some important line of discharge, which had previously served to convey the influence of the lithocyst to the undivided parts of the gonocalyx. Nevertheless we must bear in mind that this deduction is supported by no histological evidence, and that it is, moreover, very difficult to reconcile with the fact that some specimens of *Aurelia aurita* endure so enormous an amount of the most severe forms of section without suffering loss of physiological continuity between any of their parts.

The deduction also appears difficult to reconcile with another fact, viz. that in some cases (which, however, are greatly in the minority) the blocking of contractile waves in spiral strips admits, after a time, of being overcome, the contractile waves again passing from the strip into the gonocalyx as freely as they did before the section reached the point at which the blocking occurred, and this occasionally two or three times in succession. I think, however, that there is a theory by which all these paradoxical facts may be reconciled; and so at the present stage of my inquiries I provisionally accept the hypothesis of there being present in the locomotor system of *Aurelia aurita* more or less definitely integrated lines of discharge. But, in making this statement, it is almost needless to add that I wish a marked distinction to be drawn between the certainty of the hypothesis and that of the facts from which it is deduced.

Blocking of contractile waves in strips may also be caused by making a system of

interdigitating cuts in the strip itself, which system it is unnecessary again to describe. Blocking may also be caused by pressure exerted at any line which crosses the contractile strip transversely. In such cases the time during which the pressure lasts, and the intensity of the pressure while it does last, are the principal factors in determining the blockage of contractile waves, as well as the time during which such blockage will continue after the pressure has been removed. Various poisons also cause blocking of contractile waves, the obstruction to the passage of the waves being always very precisely restricted to the line in the strip where the poisoned water ends, or, if injections be used, where the injected poison is present. If a long portion of a contractile strip be immersed in the solution of a poison which will eventually cause a blocking of the waves, it is observable that for some little time before the blocking takes place the rate of transmission of the waves becomes progressively slowed.

The presence of a visual sense has been demonstrated in the case of the genus *Sarsia*, and its seat localized in the so-called eye-specks. It has also been proved that in this the first appearance of a visual organ in the animal series the rays by which the organ is affected are the properly luminous rays, and not the thermal rays beyond the luminous spectrum, as has been reasonably inferred from the position of the pigment-spot in relation to the other parts of the visual structure.

With regard to poisons, I confine myself on this occasion to briefly detailing the effects of only a few; and these effects are chosen for description in order to indicate the apparent functional identity of the locomotor centres of Medusæ, and of the relations which these centres bear to the contractile tissue of the swimming-organs, with the nervous tissue of all higher animals, and the relations which this bears to muscular tissue. Chloroform, ether, alcohol, morphia, strychnia, and curare all assert their several peculiar influences on the locomotor movements of the Medusæ, and this in all the particulars and with all the distinctness which is characteristic of their action on nervous tissues in general.

Received March 24, 1876.

Postscript III.

On the 3rd of February, 1876, I received the following communication from Dr. Lütken, of Copenhagen:—

"With reference to your interesting note in 'Nature,' November 12th, 1874, your attention is drawn to Dr. Eimer's paper on the artificial divisibility &c. in *Aurelia aurita* and *Cyanæa capillata*, Würzburg 'Verhandlungen,' vi. (1874)."

The note here referred to is one which I sent to 'Nature' in September 1874, and which was published in November of that year. In this note I described the effects, on a species of naked-eyed Medusa, of what in this memoir I call the fundamental experi-

ment*, and added a suggestion that such of the readers of 'Nature' as should have the opportunity of repeating this experiment on the other species of Medusæ during the summer and autumn months of 1875, should do so on as many species as possible. I have to regret that no one appears to have acted on this suggestion; but at the same time, I have to express my best thanks to Dr. LÜTKEN for the very valuable reference which he has supplied. Dr. EIMER's paper clearly shows that he made the fundamental observation in the case of *Aurelia aurita* and *Cyanæa capillata* quite independently of my suggestion in 'Nature;' and Dr. LÜTKEN's reference to this paper has been of special value to me from the fact that up to the time when I received it (viz. February 1876) no one in England appears to have been aware that Dr. EIMER had done any work in connexion with the nervous system of Medusæ. This ignorance is to be accounted for by the fact that the journal in which Dr. EIMER published his paper has but a very limited circulation in this country, while of the paper itself no abstract appears in the 'Centralblatt.'

The following is a full abstract of the results and opinions set forth by the paper in question.

In *Aurelia aurita* the author observed that excision of the lithocysts was usually followed by complete and permanent paralysis of the swimming-organ, while any tissue left adhering to a lithocyst continued rhythmically to contract "like the excised heart of a frog." He appears, however, to be decidedly of the opinion that the seats of spontaneity are not the lithocysts alone, but the entire crescent-shaped interruptions of the margin in which the lithocysts are lodged (see Plate 32). He arrives at this conclusion because he finds that by progressively lessening the amount of contractile tissue which is left adhering to an excised lithocyst, this amount may be reduced to a "tissue-zone" only a few millims. broad. This crescent-shaped zone, therefore, he always speaks of as the "contractile zone." Concerning the *character* of the contractions, Dr. EIMER is of the opinion that they are "usually involuntary," but that they are also in a certain degree subject to the control of the will.

The author next proceeds to detail some very interesting observations on the rate of the rhythm. He says, what is quite true, that although the pulsations of *Aurelia* are very rhythmical, they are frequently interrupted by pauses of longer or shorter duration. He says, further, that the duration of pauses bears a direct relation to the

* In some respects this description was not quite accurate, and for the following reason:—The observation was made towards the end of the summer of 1873 on some individuals of the species of *Slabberia conica*. I found that excision of the marginal bodies alone determined complete paralysis of the nectocalyx, and also, apparently, of the polypite. Next year I was unable to pursue the inquiry, but published the note in 'Nature' above referred to. Last year I continued the research, but did not happen to fall in with any specimens of *Slabberia*. From my observations on the nearly allied form of *Sarsia*, however, I am now inclined to believe that if my specimens of *Slabberia* two years before had been in a perfectly vigorous state, I should have found it necessary, in order to cause complete paralysis of the nectocalyx, to remove its *entire* margin, and not merely the vesicles alone.

previous number and strength of the pulsations. If the unmutilated animal be pricked with a needle, it endeavours to swim away from the source of irritation.

If the unmutilated animal be carefully watched while performing its locomotor contractions, it will be seen that the latter emanate from the margins of the crescent-shaped notches, *i. e.* from the "contractile zones;" upon every contraction the two sides of each zone approximate each other. Usually all the eight contractile zones contract together; but this is not always the case. Frequently the contraction originates in one or in several neighbouring zones simultaneously, and then propagates itself with lightning speed to all the others, which thereupon contract either simultaneously or in rapid succession. Thus the animal is no doubt able to steer itself in any direction it chooses.

From all this, then, it appears that a locomotor contraction of the umbrella may proceed from one, from several, or from all the zones simultaneously; but in no case can a contraction of one zone take place without being accompanied by a synchronous, or almost synchronous, contraction of all the others.

The number of contractions in a given time appeared to vary in an inverse proportion to the size of the animal. Upon excising all the contractile zones save one, the contractions were seen to emanate from this zone alone, and from thence to spread themselves all over the umbrella. On now excising this last remaining zone, all contractions suddenly ceased. Occasionally, however, there supervened several *irregular*, *inefficient*, and *feeble* contractions, which were of a more local nature. It was rarely that these contractions lasted for any considerable time; generally they ceased after a few moments, or at any rate after several hours: only in one case was it observed that they continued on the following day.

Immediately after this operation the animal usually remains motionless, as if suffering from shock, and it is only after an interval that it begins to make attempts at contractions. These attain a certain degree of vigour and then again decline. Mechanical stimulation, *e. g.* pricking the umbrella, causes in the mutilated organism responsive attempts at contraction; but sooner or later, after the spontaneity of the animal has been destroyed by excision of the contractile zones, the irritability of the contractile tissues disappears, and death of the tissues supervenes. Having placed three specimens of *Aurelia aurita* under similar conditions, Dr. Eimer removed all the lithocysts from one of them, all save one from another, and none at all from the remaining specimen. The specimen which had all its lithocysts removed began to show symptoms of decomposition (aufgelöst), while the other two specimens were still quite lively.

Next are detailed some experiments in bisecting specimens of *Aurelia aurita* through their whole diameter. It was observed that the shock which this operation entailed appeared to be more severely felt by the small individuals than by the large. It was also observed that in one experiment the two halves contracted independently, so that the number of contractions which were made in a given time by the one was no index of the number given in the same time by the other. On the day subsequent to the operation, however, both halves contracted pretty uniformly, and each half showed

a tendency to assume a bell-shape. In consequence of this slight change of form, the two halves were now able to swim at all levels in the water, and were no longer obliged, as on the previous day, to lie at the bottom of the vessel. In spite of every care these two halves died on the third day, presumably from the want of food.

By counting the rate of the pulsations in entire animals, and then dividing these animals by radial incisions into halves, quarters, or eighths, in such a manner that each portion should contain at least one lithocyst, and, lastly, by counting the rate of the pulsations of the halves, quarters, or eighths, Dr. Eimer was able to satisfy himself as to the following very important fact:—The sum of the contractions performed by all the parts of a divided animal was, in a given time, equal to the number of contractions which had been performed by that animal before its mutilation. This rule, however, was liable to very frequent variations.

Portions thus severed and kept without nourishment manifest after a time a progressive retardation in the rate of their contractions. Want of fresh sea-water also has the same effect, producing the greatest irregularity in the rate, strength, and rhythm of the pulsations. Addition of fresh sea-water revives the animal even from a state of apparent death, when the contractions return to their normal strength and rhythm.

Dr. Eimer also made the following experiments in section. From the margin of *Aurelia aurita* he carried a radial incision of several millims. long, in order to test a view which he attributes to Haeckel, viz. that all the nervous connexions in Medusæ are dependent upon a single peripheral ring. Of course he obtained negative results, and thereupon lengthened his radial section until it came within 8 millims., and in another individual within 6½ millims. from the ovarian pouch. He then found that at this point the two portions of the animal first became physiologically separated.

Next, in order to test Agassiz's view as to the presence of an upper nervous ring and the possibility in the former experiments of this ring having acted vicariously for the divided portion of the lower ring, Dr. Eimer made two radial incisions proceeding from the centre towards the circumference of the disk. He found, of course, that these sections might be carried to within quite a short distance of the margin before the portion of tissue which was included between them became physiologically separated from the rest of the umbrella.

Lastly, as a control experiment, the author cut out from the middle of an *Aurelia* measuring 10 centims. in diameter a circular mass measuring 7½ centims. in diameter, thus reducing the margin of the animal to the form of an open ring. This marginal ring continued, of course, to contract, and this at first more rapidly than usual. On the other hand, all spontaneity ceased in the other part of the animal after an interval of three hours. Dr. Eimer then submitted this open ring to a series of interdigitating cuts. He found that in no one of its parts was the physiological continuity of the tissue destroyed by the sections, although it seemed to him that the severer forms of such section tended partially to obstruct the passage of the contractile influence from one division to another—that the thinner the connecting link of tissue, the

greater was the resistance which it offered to such passage. Therefore, in view of the fact that the physiological connexions only appear to be certain so long as the connecting portions of tissue are not narrowed down below a certain point, Dr. EIMER concludes in favour of a nervous plexus pervading the contractile tissues rather than in favour of the functional homogeneity of these tissues. He observes, however, very justly, that if such a plexus is present, its fibres must be capable in a high degree of vicarious action. Dr. EIMER states further, that the amount of tissue which proves sufficient to maintain physiological continuity between any two almost severed parts differs in different portions of the umbrella.

The paper concludes with several theories as to other possible functions which the lithocysts may have to subserve as well as that of locomotion, *e. g.* respiration and nutrition; but as these theories are not supported by any observations or experiments, it seems unnecessary to adduce them here. It therefore only remains to state that Dr. EIMER has satisfied himself as to the presence of nerve-cells and fibres in the region of the lithocysts, and that in his experiments upon excision of the contractile zones in *Cyanæa capillata* he obtained results which were perfectly conformable with those which he obtained in the case of *Aurelia aurita*.

I have entered thus at length into the contents of Dr. EIMER's paper, because, as my work was throughout independent of his, it becomes the more important to state clearly the points in which we agree and the points in which we differ. It is a matter of satisfaction to me that, while the latter are but of subordinate interest, the former are throughout the more important.

First, then, as to the mere matter of priority, it may be well to state that, as Dr. EIMER's work was done in September of 1874, I have a right to claim precedence, both as to observation and publication of what I have termed the fundamental experiment. On the other hand, Dr. EIMER has the right to precedence in the case of all his other observations. I shall now consider these observations *seriatim*; and if I appear to give undue prominence to the points in which I differ from Dr. EIMER, it is only because I thus hope to secure a still more perfect agreement in our future papers.

It will, of course, have been observed that Dr. EIMER's view as to the exact seat of spontaneity in *Aurelia aurita* does not coincide with mine. He is careful to state that the ganglionic function is distributed all round what he terms the "contractile zone," *i. e.* the crescent-shaped interruption of the margin in which the lithocyst, together with its gelatinous hood, is situated (see Plate 32). On the other hand, I have stated it as my opinion that the lithocyst is alone the locomotor centre; and notwithstanding the account which Dr. EIMER gives of the experiments by which he sought to localize that centre, I still adhere to this opinion. Dr. EIMER's experiments in this connexion were twofold:—1st, that of progressively lessening the amount of contractile tissue left adhering to an excised segment of *Aurelia aurita*; and 2nd, that of excising the lithocyst without injuring the "contractile zone." Of these two methods Dr. EIMER appears

to lay most stress upon the first one; for he merely mentions the second method in a short footnote towards the end of his paper, and there states that he only tried it in a few cases. Yet to me it seems that for the object in view the second method is much more trustworthy than the first. I am well aware of the fact, pointed out by Dr. EIMER, that upon each contraction of a given segment of *Aurelia aurita* the two arms of the so-called "contractile zone" approximate each other, and that this gives rise to the appearance of spontaneous action on their part. I think, however, that this appearance is deceptive, being caused only by the absence of resistance at the interrupted part of the margin to the pressure exerted by the contraction of the immediately surrounding tissues. At any rate, so long as this possible explanation has not been thoroughly excluded by experiments conducted on the converse method of removing the lithocysts from between the arms of the contractile zone, so long, it seems to me, must the method we are considering be valueless. The question, then, must be decided by the converse method just alluded to, and by it alone. Now I have made experiments according to this method, and, so far as I remember, in every case, when sufficient care was taken to remove all the lithocysts, the contractile zone entirely ceased its contractions. And not only so, but by removing, with the aid of a well-pointed scissors, the little sac of crystals composing the central part of the lithocyst, without injuring the curious wing-like appendages by which this sac is partly surrounded, and, conversely, by removing in other specimens these wing-like appendages alone, without injuring the little sac of crystals—by these experiments I was able to satisfy myself that the whole spontaneity of the lithocyst appeared to be exclusively lodged in the minute sac of crystals referred to.

There is thus in this particular a direct contradiction between the results of Dr. EIMER's experiments and those of my own. I should therefore like to state that my experiments with reference to this subject were not made till near the end of the season, and so at a time when the only specimens I could procure were small and not very active. In view of this fact I intended to defer publishing any account of the experiments now detailed until I had an opportunity of confirming them on vigorous specimens; but a perusal of Dr. EIMER's statements appears to render it desirable for me to give an opinion now upon the point under consideration, although I confess that, for the reason just mentioned, I do so with some diffidence.

I fully agree with Dr. EIMER in his view that the contractions of *Aurelia aurita* are "usually involuntary," but that they are nevertheless to a certain extent subject to the control of volition. As stated in the beginning of this paper, I believe that different species of Medusæ are endowed in different degrees with the power of volition; and in this respect I should place *Aurelia aurita* at the head of all the covered-eyed species I have observed: its contractions are not of so purely *rhythmical* a nature as are those of *Cyanæa capillata*, &c.

But this leads us to the next observation mentioned by Dr. EIMER, viz. that the length of the pauses between any series of contractions bears a direct relation to the

number and strength of the previous contractions. This is no doubt true as a general statement, and as such is what might have been anticipated; but I do not think that a number of observations would tend to establish any more precise relation. In the case of *Sarsia* the alternations between periods of rapid swimming and periods of complete repose are much more marked than in *Aurelia aurita*, to which Dr. EIMER's tables refer; and I am sure that with them the rule in question can only apply in a very general way. It is to be observed that Dr. EIMER himself does not appear to place much reliance on particular applications of this rule.

I am able to confirm Dr. EIMER's statements as to the various ways in which the lithocysts discharge their influence relatively to one another, and would only add the curious fact that very frequently one or more of the eight lithocysts appears to be temporarily or permanently prepotent over the others—the contractions always originating in it for a great number of times in succession.

Mere observation with the eye, however, is not sufficient to determine the interesting question as to whether or not there is any further coordination between the lithocysts than is brought about by the rapid passage of contractile waves from one to the other. I have accordingly made a large number of variously devised sections with the view of answering this question; but it would occupy too much space to detail them at present. I may state, however, that Dr. EIMER is quite right in his assertion that in no case can a contraction of one zone take place without being accompanied by a synchronous, or almost synchronous, contraction of all the others; and not only so, but in all my forms of section I find it to be universally true, that as soon as a contractile wave which starts from one lithocyst arrives at another (no matter how far off or how feeble the residuum of the contractile wave may be), the latter is immediately stimulated into activity, liberates a powerful discharge, and so originates a new wave of contraction. Thus, for instance, it is not difficult to obtain a series of lithocysts connected in such a manner that the resistance offered to the passage of the waves by a certain width of the junction tissue is such as just to allow the residuum of the contractile wave which emanates from one lithocyst to reach the adjacent lithocyst, thus causing it to originate another wave, which in turn is just able to pass to the next lithocyst in the series, and so on, each lithocyst in turn acting like a reinforcing battery to the passage of the contractile wave. But, as already observed, it does not fall within the scope of the present paper to discuss the subject of coordination among the locomotor centres of Medusæ. I may state, however, that there appears to be important differences between the discophorous naked-eyed Medusæ and the true Discophora in this respect; for in all the species of the former which I have as yet observed, the area of paralysis in the nectocalyx corresponds much more precisely with the line of ganglionic tissue which has been removed from its margin than it does in the case of the true Discophora.

I cannot quite assent to the description which Dr. EIMER gives of the contractions which sometimes supervene in the umbrella of *Aurelia aurita* when all the lithocysts have

been removed. He describes them as "several *irregular*, *inefficient*, and *feeble* contractions of a local nature which rarely last any considerable time." This is no doubt partly true of some cases, but it is not true of all. I have frequently seen these after contractions as rhythmical (though this is rare), as effectual, and as powerful as those which had been previously supplied by the single remaining lithocyst. Moreover these contractions may usually be seen to emanate from some very localized portion of tissue, and from thence to radiate over the whole substance of the umbrella, just as the contractile waves which emanated from a single remaining lithocyst had previously done. On now cutting out this localized portion of tissue, the umbrella usually becomes again paralyzed, while the portion of tissue which previously animated it may be seen to continue its contractions after the manner of excised lithocysts. I did not pay sufficient attention to the number of hours after excision of the lithocysts during which these secondary movements continued, to admit of my speaking with confidence on this point; but so far as I can recollect my numerous experiments with this species, it is certainly not correct to say that these contractions "generally ceased after a few moments." My impression is that they *usually* last for several days. I agree with Dr. EIMER, however, that, as a general rule, the secondary movements in *Aurelia aurita* are not so persistent as the primary ones, and also that in this species, under some circumstances, insensibility to stimulation rapidly supervenes upon loss of spontaneity. This, however, is far from being always the case with *Aurelia aurita*, and is not even generally the case with some other species—*Cyanæa capillata*, for instance, continuing to respond even to slight stimulation *two or three days* after it has been completely paralyzed by the removal of its lithocysts, and this even though it be kept in a small jar without change of water. Again, if the lithocysts be left *in situ* and the animal be kept in a confined body of water, irritability will continue for days after all the usual indications of spontaneity have disappeared. Nevertheless, with but slight modifications, I have confirmed Dr. EIMER'S experiment of placing different specimens of *Aurelia aurita* under similar conditions, removing the lithocysts of some and not of others, and observing that those individuals which had been operated upon died sooner than those which had not.

These experiments, however, and many others entailing similar precautions, I do not intend to publish until next year, when I hope to have the opportunity of conducting them in a more satisfactory manner.

I am also able to confirm Dr. EIMER'S statements regarding the behaviour of bisected *Aureliæ*; and I think with him that it is not improbable that halves, quarters, or eighths of such Medusæ would, under suitable conditions, redevelop into entire animals.

Dr. EIMER'S very interesting statement, to the effect that an *Aurelia* before its mutilation contracts twice, four, or eight times as rapidly as do its half, quarter, or eighth part after mutilation, is a statement which I am unable either to confirm or to dispute. I did indeed observe, in a general way, that the smaller segments of an *Aurelia* manifested a slower rhythm than the larger segments; but it never occurred to me to test

for any constant relationship. Dr. EIMER, indeed, is careful to state that the relationship he points out is one that is liable to very frequent exceptions; but even if it were found only to apply to a tolerably large percentage of cases, it would be relationship full of interest to the physiologist.

It is needless to say that there is a complete agreement between Dr. EIMER and myself as regards the results of section.

Concerning Dr. EIMER'S histological observations, it is, of course, impossible for me to say any thing; for he neither figures nor describes the elements which he regards as nervous. They may therefore or may not correspond with appearances which I have myself observed.

It only remains to notice Dr. EIMER'S statement with reference to *Cyanæa capillata*. He says that the effects of the fundamental operation upon this species were precisely similar to the effects of it upon *Aurelia aurita*, whereas in my experience it was not so. As already stated, I found these effects to be *analogous*, but not *identical*—*Cyanæa capillata*, *as a rule*, being less frequently or less completely paralyzed by excision of its lithocysts alone than was *Aurelia aurita*. I can only explain this discrepancy between Dr. EIMER and myself by the fact which he states, viz. that he performed but few experiments on *Cyanæa capillata*.

In now concluding this somewhat elaborate postscript, I wish it to be understood that I have mentioned the various points in which Dr. EIMER and myself do not quite agree, only because I think it is for the benefit of the subject on which we are both engaged that such differences should be noted before the work of another year begins. In this way, when opportunity again affords, we may both be able to repeat such of our observations as are now rendered doubtful by want of complete accordance.

G. J. R.

EXPLANATION OF THE PLATES.

PLATE 32.

Aurelia aurita, $\frac{1}{2}$ nat. size. The animal is represented in full diastole, with its polypite removed. In some details the drawing is not quite accurate.

PLATE 33.

Aurelia aurita, with polypite and seven lithocysts removed, submitted to spiral section.

XII. *On the Refraction of Sound by the Atmosphere.*

By Professor Osborne Reynolds. *Communicated by Professor* Stokes, *Sec. R.S.*

Received November 22, 1875,—Read January 6, 1876.

In a paper read before the Royal Society, May 1874, I pointed out that the upward diminution of temperature in the atmosphere (known to exist under certain circumstances) must refract and give an upward direction to the rays of sound which would otherwise proceed horizontally; and it was suggested that this might be the cause of the observed difference in the distinctness with which similar sounds are heard on different occasions, particularly the very marked advantage which night has over day in this respect. At the time at which that paper was written no direct experiments or observations had been made to verify the truth of this suggestion, and therefore its probability rested on its reasonableness. Since that time, however, I have carried out a series of observations and experiments which, although far from complete, throw some light on the subject, besides revealing some remarkable facts. I hope to be able to continue the investigation; but since its nature is such as to render the chance of bringing it to any thing like a final conclusion very uncertain, it seems to me that it may be well to publish an account of what has been already done; and this is the object of the present communication.

In order to render the object of the various experiments clear, it may be well to recapitulate here some of the theoretical considerations previously explained. It will be remembered that the idea that the variations of temperature would cause refraction of sound occurred to me while making experiments on the effect of wind upon sound, from which it was shown that when sound proceeds in a direction contrary to that of the wind, it is not, as had been thought, destroyed or stopped by the wind, but that it is lifted, and that at sufficiently high elevations it can be heard to as great distances as in other directions, or as when there is no wind—thus confirming the hypothesis first propounded by Professor Stokes and afterwards by myself, that the effect is owing to the retardation of the velocity of the wind near the earth, which allows the sound moving against the wind to move faster below than above, and thus causes the fronts of the waves to incline upwards, and consequently to move in that direction. Having clearly shown that this was the case, it became apparent that any thing which would cause an upward diminution in the velocity at which sound proceeds would cause a similar effect to that of the wind and lift the sound, and that since the speed of the sound depends on the temperature of the air in which it is moving, an upward diminution in the temperature must cause such an effect. That such a diminution of temperature does very

often exist was proved by Mr. GLAISHER's balloon ascents in 1862, in which he found that when cloudy the mean rate of diminution for the first 300 feet was 0°·5 for each 100 feet, and that when clear it was 1°, and that on some occasions it was greater and on others less than this. A variation of 1° in the temperature of the air alters the velocity of sound nearly 1 foot per second, so that with a clear sky the sound instead of moving horizontally would move upwards on a circle of 110,000 feet radius, and with a cloudy sky on a scale of 220,000 feet radius. This rate of refraction is very small compared with that caused even by a very moderate wind; and consequently in order to verify it by experiment it is necessary to observe sounds at much greater distances. This renders the experiment very difficult to carry out; and to make it worse we have no means of determining what the upward variation of temperature is, which therefore can only be surmised by the behaviour of the sound.

The method of experimenting which first suggested itself was the same as that which I had previously employed for wind—namely, to obtain a means of producing a sound of certain intensity, and proceeding to such a distance that it could no longer be heard at the ground or on the level, and then ascertaining whether the range was extended by attaining a greater elevation or elevating the source of sound.

The difficulty in every item of the experiments was greatly enhanced by the increased distance. For the wind an electric bell had answered very well, the range on the level being always less than a quarter of a mile; but where the range was to be measured in miles, something in the nature of an explosion was the only sound available. A place in which to make the experiments was also difficult to find; for it involved a range of several miles of level and unobstructed country, and thus the time occupied in moving from place to place became a matter of serious inconvenience. The greatest difficulty of all, however, was the effect of the wind; since this was much greater than any thing to be expected from the temperature, it was absolutely necessary that the air should be quite calm, a circumstance which no precaution will insure, and for which, as I know from experience, one may have to wait a long while. These various circumstances rendered the results of the first series of experiments less conclusive than I had hoped they might prove.

Experiments with rockets.

I obtained a quantity of rockets capable of rising to a height of 1000 feet and exploding a charge of 12 ounces of powder. The first experiments with these rockets were made at Debach, a village lying between Ipswich and Framlingham, where the country is tolerably flat and traversed by roads in all directions.

I. On the 14th of July, at about 3 P.M., three rockets and three cartridges were fired from the same spot, observers being stationed at three quarters of a mile and a mile and a half respectively. There was no wind, but the sky was covered with a thick haze, the day being very hot. All six discharges were heard at the nearer station, but only the rockets the distance of a mile and a half, although these were heard very distinctly, even their hiss as they ascended.

II. On the 16th of July, at 3 P.M., the day being very hot with no wind, a single rocket was sent up, an observer being stationed at four miles and a half on the Woodbridge road. The explosion was very distinct, but the hiss was not heard.

III. On the 18th a series of rockets were compared with the discharges of a gun capable of firing ¼ lb. of powder, and which made a much louder report than the rockets. The observers drove along the Framlingham road, the times of the discharges having been determined beforehand. This road was chosen because at the commencement of the experiments the wind was blowing almost at right angles to it. The wind was very light when the start was made, but before the first gun was fired it had considerably strengthened and changed in direction so as to blow against the sound. It was to this cause I attribute the fact that the first two guns were not heard at a distance of a mile and a half and two miles respectively. After this the direction of the wind again changed, and the two next guns were heard distinctly, although at greater distances; but, strange to say, the rockets at the same distance were not heard. The wind remained constant in this direction until the end of the experiments, and a rocket was heard at four miles. Owing to the changes in the wind the results of these last experiments have shown nothing as regards the refraction of sound, although they show (what was, indeed, shown by the previous ones) that it is possible on a very hot day when there is little or no wind to hear the discharge of a small cartridge, such as that carried by the rockets, distinctly for a distance of four or five miles, and this when the lower stratum of the atmosphere was so heterogeneous that all distant objects near the ground appeared to waver and twinkle as they do when seen over the top of a furnace.

In the hope of improving the conditions of the experiments, I accepted the invitation of my friend Major Hare, of Docking in West Norfolk, to accompany him in his yacht the 'Feronia' during a cruise on the east coast, taking rockets with me. Here I spent three weeks without having a single calm day.

Experiments in Lynn Deeps.

On the evening of the 18th of August, however, the weather improved; and being then in Lynn Deeps, I made some preliminary experiments so as to get the men into the way of firing the rockets. The yacht was at anchor in what is called the Upper Road, and at 9.50 P.M. I rowed with two men in a direction slightly to leeward of the yacht. The wind was very light: at a distance of two miles they fired a large pistol; the interval between the flash and the report was eleven seconds (which gave us our distance); the report was loud and accompanied with prolonged reverberation; a rocket was also heard distinctly, but was not so loud as the pistol, and was not accompanied with any echoes or reverberation. The hails from the yacht were heard by us in the boat quite distinctly, but our answers were not heard on board the yacht. As there was a light mist it was not thought safe to go further away from the yacht, so we returned and waited in hope of being able to do something the next day. In this we were not disappointed; for on

this day we observed what I have no doubt will be thought an extraordinary phenomenon, although not of the kind anticipated.

The morning was perfectly calm, with only a few local breaths, which, measured with the anemometer, never registered more than two miles an hour, and came first from the east and then from the west, but not from the north. Up to 12 o'clock the sky was completely covered with a white cloud, which did not show the least sign of movement. The land from four to eight miles distant was hazy; the thermometer stood at 65° in the cabin with all the lights open. The Upper Road, in which the 'Feronia' was anchored, is two miles below the ends of the stone banks which terminate the Lynn Cut, and five miles from Lynn (see accompanying chart, Plate 34). From this station sounds in Lynn were distinctly heard. Steamers could be heard leaving the dock.

About 12 o'clock the sky cleared, and a slight breeze (four miles) sprang up. We then weighed anchor and proceeded down the Bull-dog Channel. Soon after the sky became perfectly clear, and the breeze died away until the yacht had not steering-way. I then had a boat lowered (with the same two men), and proceeded to row to the Roaring Middle Buoy, while the yacht still continued her course as well as she could down the Bull-dog Channel; she was going north by east in a curve, while we were going north-west. Before leaving the yacht I arranged that on our showing two flags they should send up a rocket, and when one they should fire a pistol, and that whenever they heard us call they should answer. When at about half a mile distant I commenced calling, and the answers came back quite distinct; when a little further some one on the yacht commenced tapping the anchor, and we heard this quite distinctly until we were nearly two miles off them; then the tapping was discontinued, and I commenced calling again. Each time the answer came back quite distinct at the instant it was expected, and afforded a good means of checking our distance, which we also knew from the buoys. At two miles, although the calls were quite distinct, I signalled for a pistol; the report was loud. The sun was very hot to us in the boat—so hot, indeed, that it blistered the skin on my hands and face.

The next time I called, the answer was doubtful; but on my calling again, it came quite distinct in thirty seconds. I then signalled for a pistol, and heard a report which we took to be a pistol, but afterwards found to be a rocket, we being too far off for them to distinguish our signals. I then asked for a rocket, and had one, of which we heard the hiss as well as the report. We now proceeded up to the Roaring Middle Buoy and signalled for rockets and pistols, but could get neither, so we judged that they could not see our signals. Although it seemed hopeless, I called from this point, and to my surprise we all heard the answer faint but quite distinct after an interval of thirty-five seconds. It was now about 3 P.M., so that we had been rowing about two hours and a half. We waited at the buoy and kept calling; but as there were now a number of fishing-boats which answered our calls we could not be certain of an answer. At this time our calls appear to have been heard on the yacht but not answered. When we heard the last call, to be sure of it, the yacht was close by the Sunk Buoy; she was now

approaching the Well light-ship, which is six miles from the Roaring Middle Buoy. There was now a very light breeze again, so we set up our sail to get steering-way on, and fell down with the tide. We presently heard a rocket go up and explode, but we could make no impression with our signals: we found on returning that they had completely lost sight of us; nor was this surprising considering that we were in a small boat and the sun was directly behind us. A breeze sprang up, so we returned to the yacht, where on comparing notes we found that we had heard every call as well as report. During the interval in which we had no answers, Major HARE, who had been answering my calls, having completely lost sight of us, had gone below to get some lunch; in the mean time the men on deck had heard our calls, but not having instructions had not answered them.

To sum up the results of our excursion:—We had called and been answered up to three miles and a half, and our calls as well as the reports of the rockets had been heard to more than five miles.

Incidentally I noticed that we could occasionally hear the reports of guns from the shore, which was more than eight miles distant; and once while listening for an answer to one of my calls, I distinctly heard a dog bark, which must have been on shore, as there was no boat between us and it except the yacht. All the time we could distinctly hear the paddles of a steamer, which at the time we were at the Roaring Middle was in the Wisbeach Channel, or nine miles from us and fifteen from the yacht, on which her paddles were also distinctly heard.

It appears to me that the distances at which sounds of such comparative low intensity were heard over the water this day is beyond any thing definitely on record. One hears casually, however, of remarkable instances: once in this district I heard of a clergyman who from the Hunstanton side of the Wash heard a man hammering a boat on the Wisbeach side. When one thinks, however, of the extreme difficulty of identifying a sound with its source at three or four miles distance, it is no matter of surprise that such phenomena should for the most part escape notice. On this day, had we not been purposely on the look out, I do not think any thing we heard would have attracted our attention. I have often heard the rifles of volunteers over tolerably flat country seven miles; and, as I have previously stated, the guns of the naval review at Portsmouth were heard by many persons, including myself, in Suffolk, over a distance of 170 miles*.

With regard to the cause of the exceptional distances over which we heard the sounds on the 19th of August, 1874; as was only natural, my attention was all the while directed to this. For the sake of my experiments, what I had been in hope of was a state of the atmosphere which would cause great upward refraction of the sound, and I was naturally on the *qui-vive* for any indications of such a state. All the morning I had been watching the distant objects to see whether they were lifted or depressed by the refraction of light. They loomed to a remarkable degree, which showed that the upward

* They were also heard by Sir WILLIAM THOMSON, who was on board his yacht about 10 or 15 miles to the west of Portland, and therefore 180 miles from Dover.

variation of temperature was the reverse of what I wanted; and before leaving the yacht I had my doubts of our finding much upward refraction of sound—of our being able to hear the rockets further than the guns. I was in hopes, however, that as the sun came out matters might change, and while in the boat I kept looking out for signs of depression in the distant objects. These, however, never came; they loomed all the time, and very considerably. From the boat we could see the water for five or six miles. The yacht's hull was visible to us all the time. On one occasion we had two buoys and a ship in a line, the nearest buoy being two miles from us; we could see the water between this and the second, and again between this and the ship.

It seems to me, therefore, that although in a manner the reverse of what was expected, our observations this day prove the very great effect which upward refraction has on the distances at which sounds can be heard. The looming of the distant objects showed that the air was colder below than above. This would tend to bring the sound down and intensify it at the surface of the water—in fact convert the sea into a whispering-gallery.

No other explanation appears to hold good. The conditions were exactly those which have been described as favourable to acoustic opacity; the sea was calm, there was no wind, and an August sun was shining with its full power, and, having evaporated the clouds, must have been raising vapour from the sea.

During the experiment I particularly noticed the echoes. Except the first and only pistol, none of the reports were attended with echoes or reverberation. But in most cases, though not in all, after calling I could hear the ring of my voice for ten or eleven seconds; and on one or two occasions when there were boats within half a mile of us, I could distinctly hear the echoes from them. Without attempting to explain the reverberation and echoes which have been observed, I will merely call attention to the fact that in no case have I heard any attending the reports of the rockets, although they seem to have been invariable with the guns and pistols. This fact suggests that these echoes are in some way connected with the direction given to the sound. They are caused by the voice, trumpets, and the siren, all of which give direction to the sound; but I am not aware that they have ever been observed in the case of a sound which has no direction of greatest intensity.

Arago's *Experiments*.

These observations in Lynn Deeps were the last I made in 1874. In the spring of this year my attention was called to a phenomenon recorded by Arago, which was noticed during the celebrated experiments on the velocity of sound made by Humboldt, Arago, Prony, Gay-Lussac, and others, on the nights of the 21st and 22nd of June, 1822, between Villejuif and Montlhéry. On both these nights the sounds from Montlhéry were heard more distinctly at Villejuif than the sounds from Villejuif at Montlhéry, although the wind was blowing (very lightly) from Villejuif to Montlhéry, the speed of the wind being about one foot per second, or, roughly, three quarters

of a mile an hour. This remarkable want of reciprocity was much commented on by the observers, although they appear to have been entirely at a loss to account for it.

On reading M. ARAGO's report*, I noticed that the observations on the barometer showed Montlhéry to be about 80 feet above Villejuif, and it occurred to me that this difference of elevation might afford a clew to the mystery. I had observed in my observations of the effect of wind upon sound that a difference of a few feet in the height of the observer or in the source of sound, especially when near the ground, often made all the difference between hearing distinctly and not hearing at all. It appeared to me probable, therefore, that there might be something advantageous in the situations of the gun at Montlhéry and the observers at Villejuif over the situations of the gun at Villejuif and the observers at Montlhéry. I was confirmed in this impression by a fact mentioned by ARAGO, viz. that on the first night the gun at Villejuif had been pointed upwards at a considerable angle, but that thinking this might have had something to do with its not being heard so well as the other, on the second night it was brought down to the horizontal. The result, however, was that the gun was not heard so well on the second night as it had been on the first. This remark concerning the gun at Villejuif seemed to imply that it was fired from level ground and at no great elevation, whereas at Montlhéry it seemed possible that the gun might have been fired over a parapet. To settle this question I took an opportunity last Easter of walking over the ground from Villejuif to Montlhéry, and by the aid of a map made a section of it.

The two stations are visible from each other; that at Villejuif is on the top of a gently rising hill, whereas that at Montlhéry is on the top of a very steep sugar-loaf hill, terminating in the mound of an old castle, which is supported on the side facing Villejuif by a wall some 20 feet vertical, and then so steep that Villejuif can be seen over the tops of the trees surrounding the castle. Part of the old parapet wall is left, and it is impossible to believe but that any one firing a gun from that spot would place it with its muzzle over the parapet. It seems very probable, therefore, that the gun at Montlhéry was fired over the parapet, which would be the most favourable position for being heard, as the direct sound would be strengthened by that reflected from the wall below it, while the observers, standing somewhat behind the parapet, would not have the advantage of any reflected sound, and would therefore be in a disadvantageous position as compared with the muzzle of the gun. At Villejuif the case would be different; the gun, as fired on level ground, would be at a disadvantage compared with the observers, whose ears would be considerably above it. That this difference was sufficient to affect the results seems to have been proved by the evil effect of lowering the muzzle of the gun †.

* Annales de Chimie, 1822, p. 211.

† From my previous experiments on the effect of wind upon sound, I had been led to the conclusion that under certain circumstances there may be an absence of reciprocity in the passage of sound backwards and forwards between two points. Lord RAYLEIGH, however, pointed out to me that there are strong reasons for believing that this is not the case. To prove the force of these reasons, I made some observations behind a large wheat-stack standing alone on level ground, experience having shown me that a wheat-stack from its

These differences in the conditions of the guns and the observers would seem to afford good reason why the guns from Montlhéry should have been better heard than those at Villejuif, supposing other conditions for the transmission of sound to be equally favourable both ways; but the wind was blowing from Villejuif to Montlhéry, and that this should not have reversed the effect is the most remarkable part of the phenomenon. This is remarkable, however, only on the supposition that the effect of the wind upon sound is invariable. As it seemed to me that there were several good reasons for supposing that this is not the case, I thought it might be worth while trying a few observations. I accordingly made some experiments with my electric bell on some very calm nights in May and June, with the following results:—

When the sky was cloudy and there was no dew, the sound could invariably be heard much further with the wind than against it, even when the wind was not more than one foot per second.

But when the sky was clear and there was a heavy dew, the sound could be heard as far against a light wind as with it, and sometimes much further. On one occasion, when the wind was very light (about 1 foot per second at 6 feet above the ground) and the thermometer showed 39 degrees at 1 foot above the grass and 47 at 8 feet, the sound was heard at 440 yards against the wind, and 270 yards with it.

Now the nights on which Arago made his experiments were clear; there was a heavy dew, and the thermometer at Montlhéry showed that at that elevation the temperature was 2° F. greater than at Villejuif; so that after the experiments just described there is nothing surprising in the fact that the wind did not produce much effect on the sound.

A good reason (as I have previously stated) may be given in explanation of these changes in the effects of the wind. The wind tends to lift the sound proceeding against it and to bring down that which is travelling with it. These effects are greatest near the earth and diminish as we proceed upwards (for the simple reason that the retardation of the wind is greater near the surface). The effect of the wind, therefore, will be to intensify the sound proceeding against it at sufficiently high elevations (this was found to be the case in my first experiments) and to weaken the sounds proceeding with it at points at some height above the surface—that is, when the sound which is brought

rough surface is a most effectual barrier to sound—sound produced close to one side of the stack being quite inaudible on the other side. On this occasion, however, I found the most perfect reciprocity; sounds produced close behind the stack could be heard at a distance just as well, and no better, than similar sounds at a distance could be heard behind the stack, provided always that great care was taken to bring the ear behind the stack into exactly the same position as that previously occupied by the source of sound. It appears, however, that a few inches difference in the position of the ear on the source of sound was sufficient to make all the difference as to the audibility of the sound. These experiments therefore, although they confirmed Lord Rayleigh and showed my previous idea to have been wrong, suggested another explanation of the phenomenon which had led me to it. They show that the apparent absence of reciprocity was in reality caused by my not having taken sufficient notice of small difference in the position of the ear and the bell, and they suggest that the apparent want of reciprocity in the experiments made at Villejuif and Montlhéry was due in the same way to the small differences in the positions of the guns and the ears of the auditors, as pointed out in the text.

down is destroyed by the roughness of the surface, though over a calm sea, the sound brought down would roll along the surface as in a whispering-gallery. Now when the temperature diminishes upwards, as it does generally during a calm day, the effect of the refraction thus caused will be to increase the effect of the wind on sound moving against it, and to diminish that on the sound moving with it. But when the diminution of temperature is downwards, as it was at Villejuif and Montlhéry, and as it always is near the earth on a clear dewy night, it will directly diminish the effect on sound moving against the wind, and increase it on the sound moving with the wind. That is to say it will prevent the wind lifting the sound in one direction and will aid it in bringing it down in the other. Thus it will prolong the distance to which sound can be heard against the wind, and diminish that at which it can be heard with the wind (when the surface is rough); and when the downward diminution of temperature bears a certain relation to the strength of the wind, it is easy to see that it may neutralize or even reverse its effect.

These facts, all taken together, appear to me to afford a satisfactory explanation of the phenomenon observed by ARAGO. There was, however, one other phenomenon observed during the same experiments on which I will venture a word in explanation.

The reports of the guns at Montlhéry as heard at that station were attended with prolonged echoes, but it was not so with those at Villejuif. This phenomenon was not explained by the experimenters; but I think it admits of a simple explanation. The ground surrounding Villejuif towards Montlhéry is very flat with not a tree upon it for miles, and being all arable would at that time of the year be covered with crops. Around Montlhéry the country is hilly, some of the hills rising 100 feet above Montlhéry itself; their sides are in many places precipitous, and are largely covered with trees. From the flat country around Villejuif there would arise no echoes, but from the hills and trees around Montlhéry it is quite certain that there must arise very considerable echoes; and hence it seems to me that the phenomenon becomes simple enough.

The Report of the American Lighthouse Board.

I may remark, in conclusion, that I have just received a copy of the Report of the American Lighthouse Board, kindly sent me by Dr. HENRY, the Chairman of the Board. In an Appendix to this Report, Dr. HENRY has given an account of his experiments on the transmission of sound, undertaken for the Board, and extending over the last thirty years. These experiments have led him to the conclusion that the differences in the distances at which the same sound can be heard at different times are in all cases to be explained by refraction. He has ascribed the cause of the refraction to the wind; and to explain cases in which the refraction did not accord with the direction of the wind, he points out that it is not sufficient to know the direction of the wind at the surface, but that in order to say what would be its effect upon sound, we should know in what direction it is blowing above; for it is not the simple motion of the wind which affects sound, but the difference between its motion above and below. This is very true; and

I have met with instances at night which have led me to apply the same explanation. Many of the phenomena, however, to which Dr. HENRY has applied this explanation are, I feel sure, to be attributed to the effect of the upward variation of temperature. Dr. HENRY does not appear to have been aware of this cause of refraction of sound while making his experiments or drawing up his Report; but in a note at the end he expresses his general agreement with the views stated in my previous paper.

The Heterogeneity of the Atmosphere.

With respect to the stoppage of the sound by the heterogeneity of the atmosphere, Dr. HENRY expressly states that through all his long experience he has never met with a single phenomenon which he can fairly ascribe to this cause; and so far as my experience goes it agrees with that of Dr. HENRY. I am far, however, from thinking that there is no such effect; on the contrary, under circumstances such as those which HUMBOLDT describes as having led him to the idea, it seems to me that it must exist, but that it must at all times be confined to a very small distance above the earth's surface and be over land. That it is the principal cause, or even an important cause of the phenomena under discussion, appears to be more than doubtful; for not only does the necessary effect of refraction appear to be a sufficient cause for these phenomena, and therefore to afford a complete explanation of them, but it is very difficult to conceive the existence of a state of heterogeneity in a calm clear atmosphere at a considerable elevation above the level of the sea.

In the first place such a state of heterogeneity could hardly fail to be observed; for it would necessarily impart a flickering and unsteady appearance to objects seen through it—an effect which may be observed any hot summer's day when looking at objects low down over dry land. Over the sea, however, such an appearance has not been recorded; and although I have often looked for it, I have been entirely unable to detect it. And in the second place, even supposing the air to be in a heterogeneous state at any given instant, such a state could not be maintained many minutes; for different gases, or different portions of the same gas at different temperatures, mix and diffuse very rapidly. It is true that the heterogeneity might be maintained by upward streams of heated air or vapour, and this is doubtless the cause of the heterogeneity of air over dry hot ground; but this heterogeneity, although very apparent near the ground, is never observed at any considerable height. Upward streams of heated air must tend to mix and diffuse rapidly, and the air as it rises is cooled by expansion until it must soon cease to be lighter than the surrounding air. That, as a rule, there are no streams of heated air ascending to any considerable height over land, is definitely proved by the fact that the light smoke from burning weeds never, or very seldom, attains an elevation of any thing like 100 feet. I have often been struck with the way in which such smoke will creep along the ground for the distance of half a mile, and even then not extend to an elevation of more than 20 or 50 feet. Over the sea the cause of such streamlets must be much less potent than over land, and their existence still more unlikely.

Fig. 4*

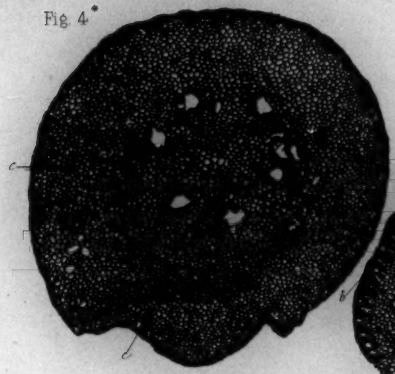
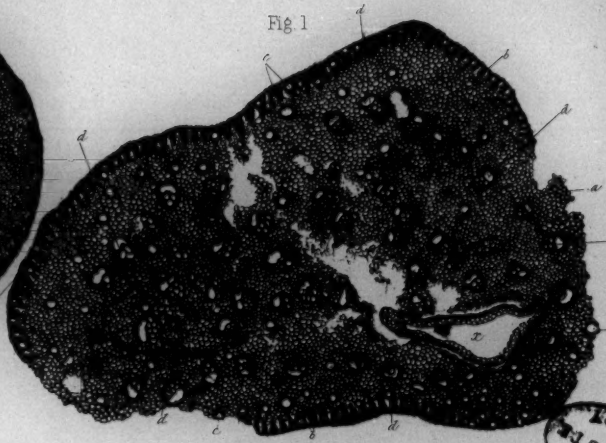


Fig. 1



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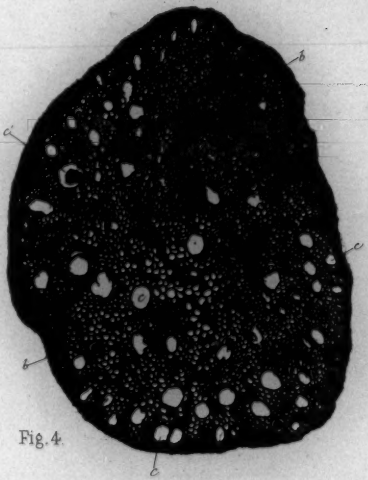
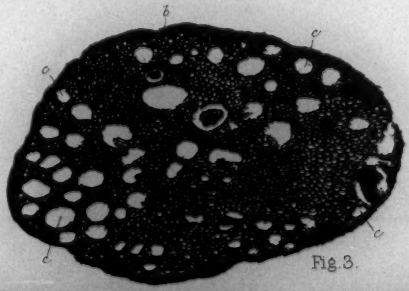


Fig. 4.

Fig. 12.



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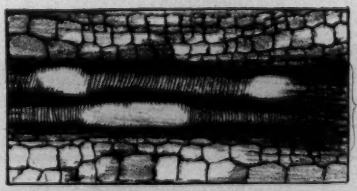

Fig. 10

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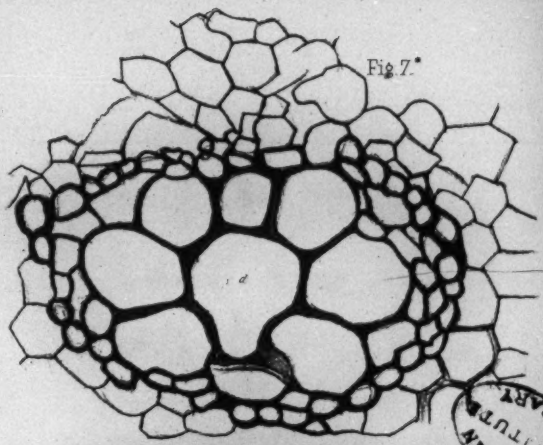
Fig. 5.



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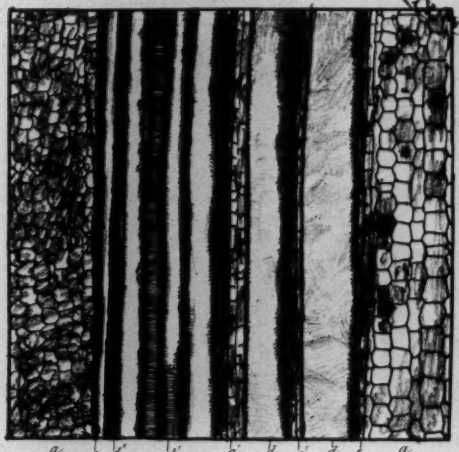

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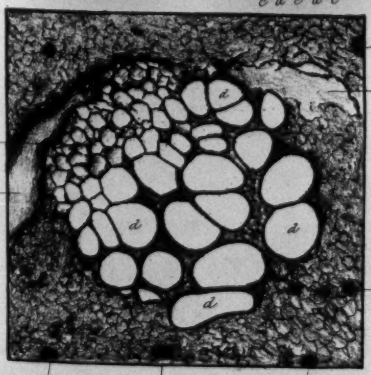

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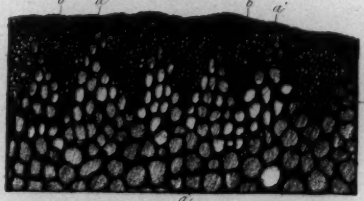
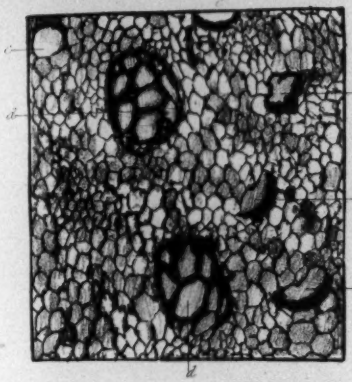


Fig. 16.

Fig. 11



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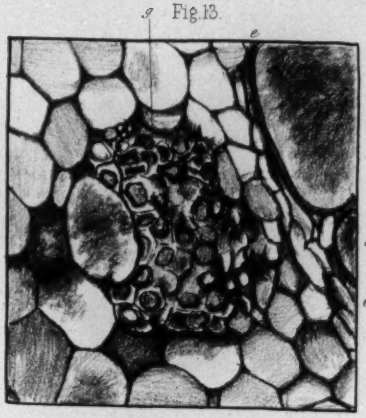

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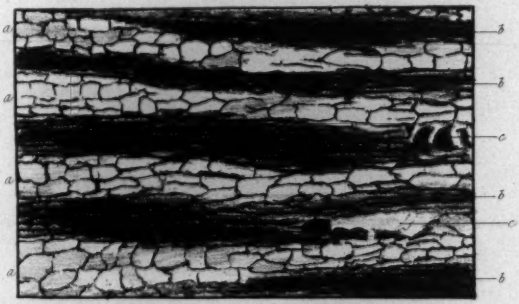
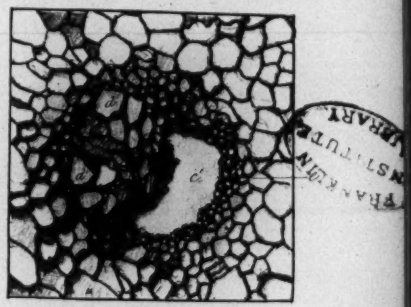
Fig. 15.





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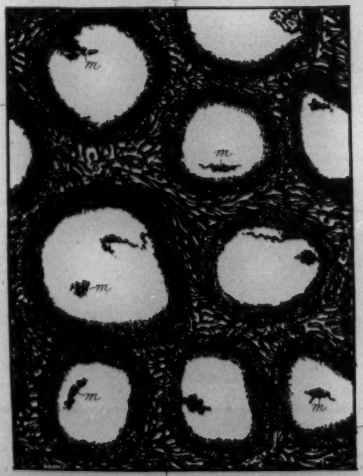

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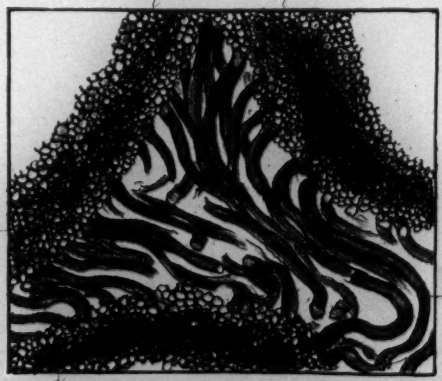

Fig. 21.

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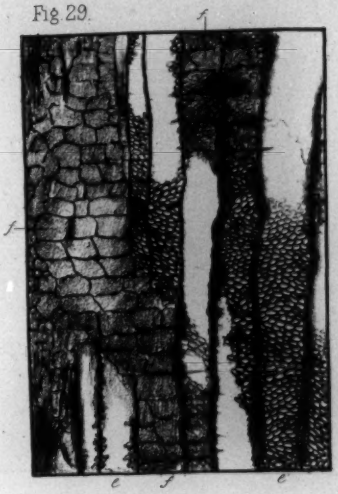
Fig. 29.



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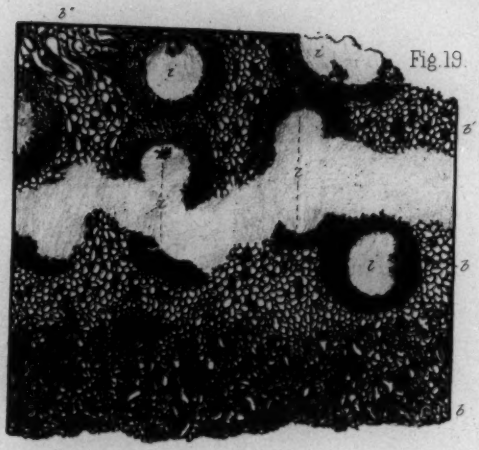

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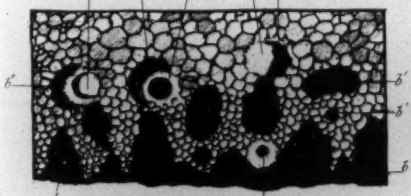

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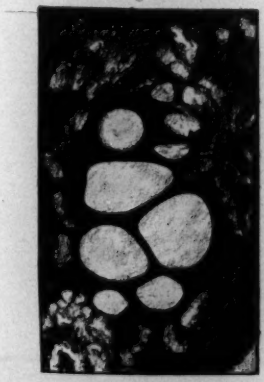

Fig. 22*

Fig. 22**

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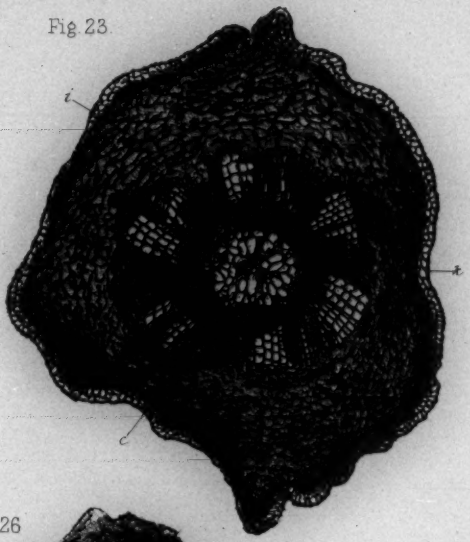
Fig. 23.



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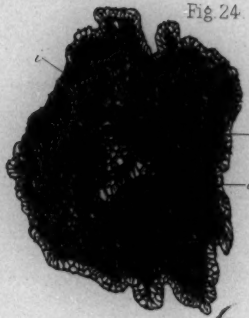

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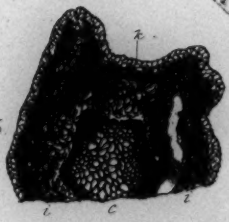

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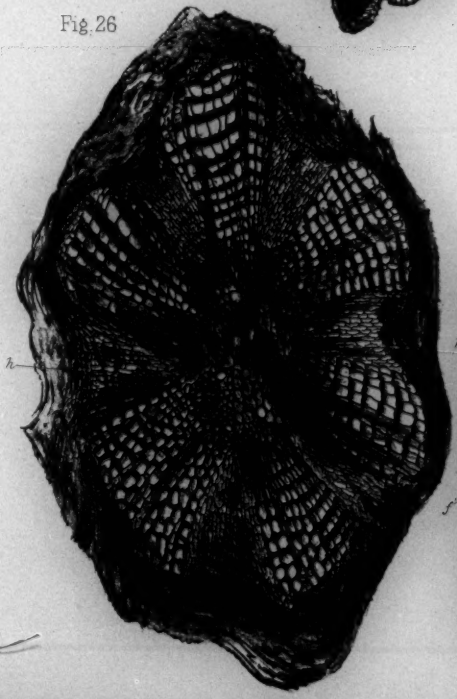

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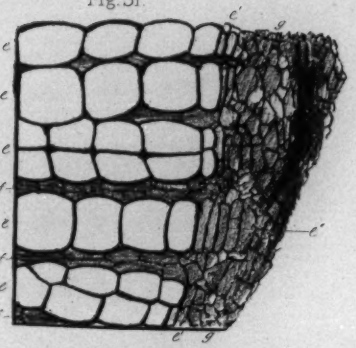

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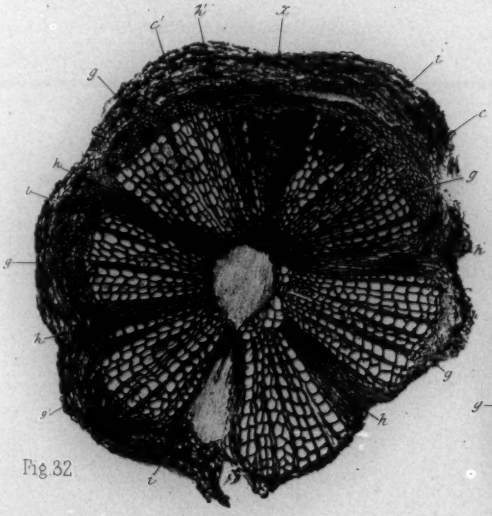

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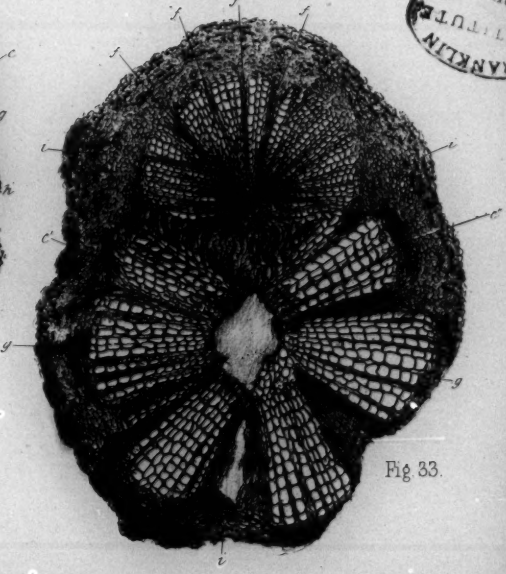

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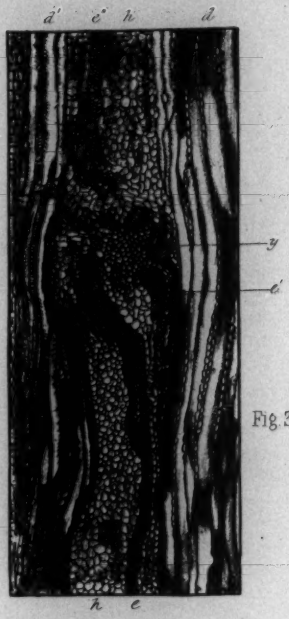

Fig. 35.

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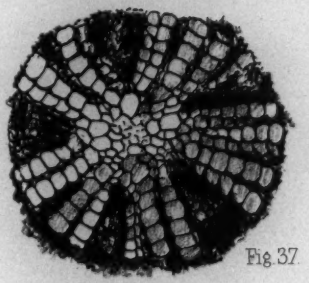

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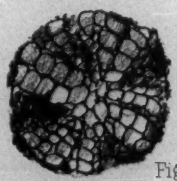

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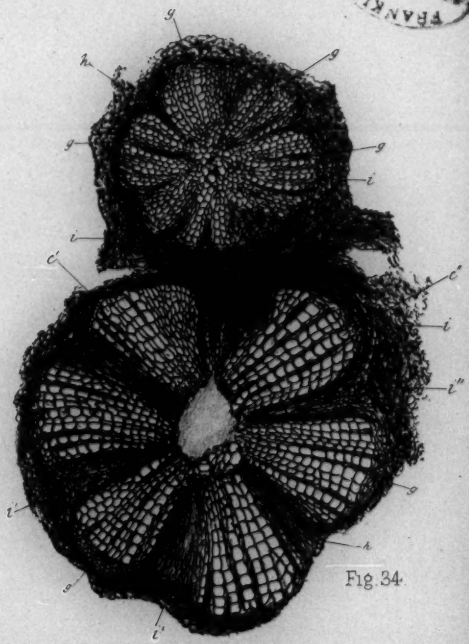

Fig. 34.

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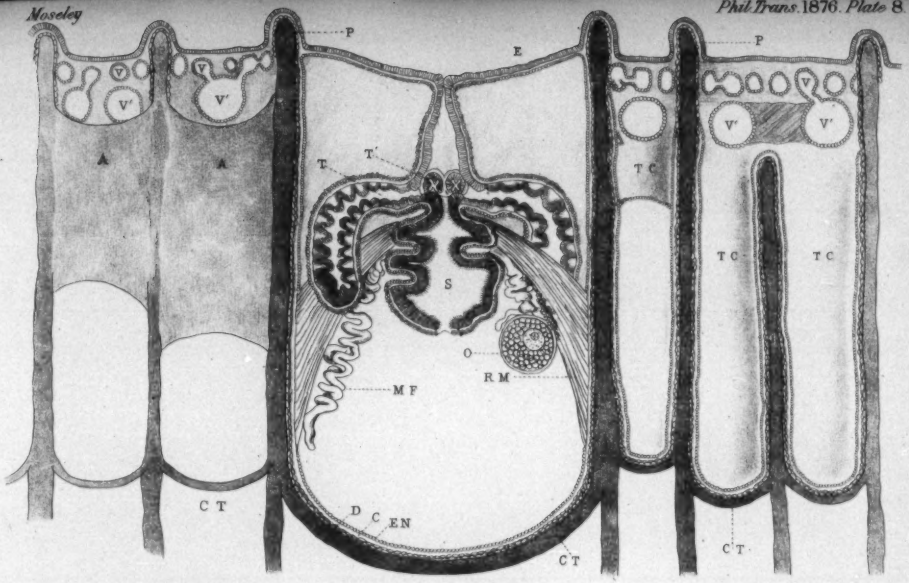

Fig.1. x 42 diameters

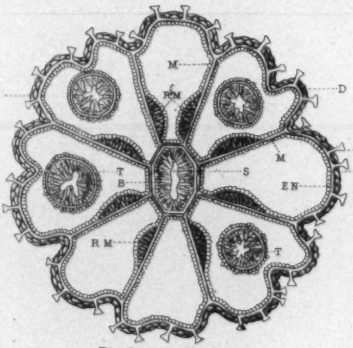

Fig.3. x 50 diameters

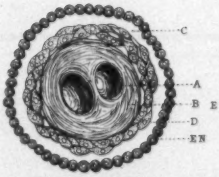

Fig. 6. x 200 diameters

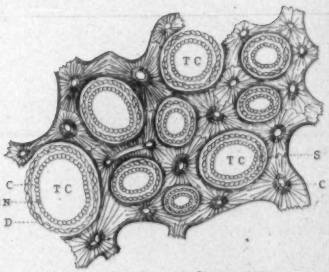

Fig. 4. x 40 diam

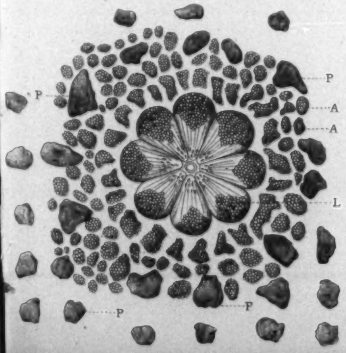

Fig.5. x 25 diameters

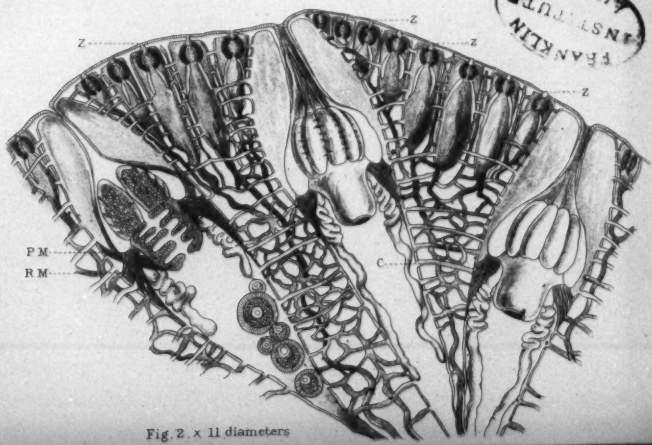

Fig.2. x 11 diameters

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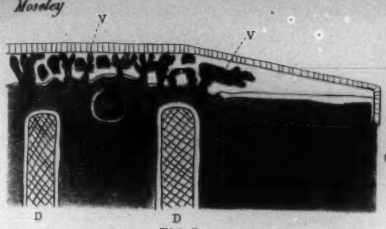


Fig. 7.

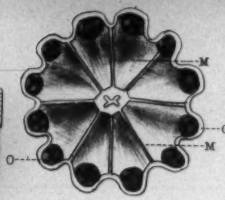


Fig. 8. × 20 diameters.

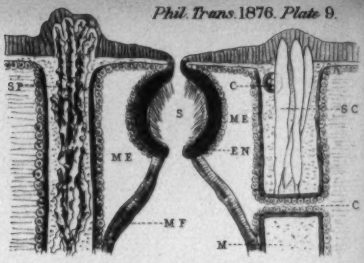


Fig. 9. × 60 diameters

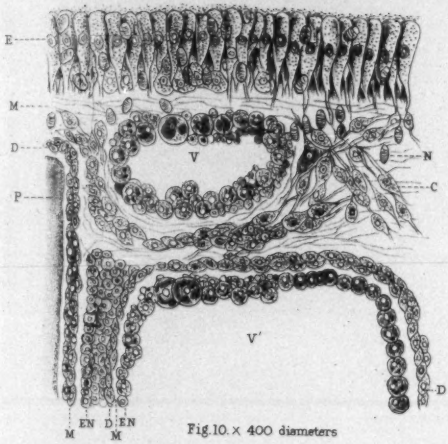


Fig. 10. × 400 diameters

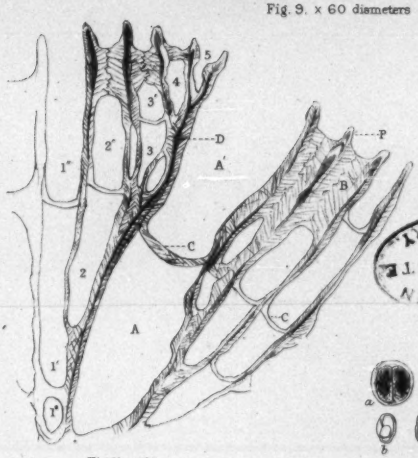


Fig 11. × 15

Fig. 13.
a × 670, b × 830 diam.

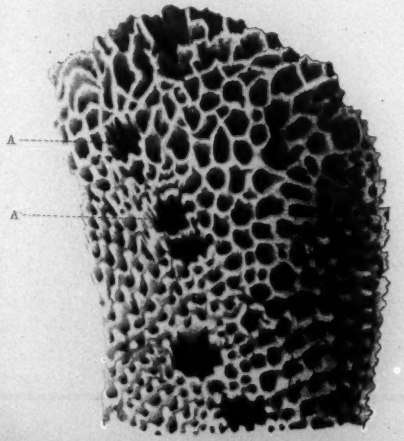


Fig. 16. × 8

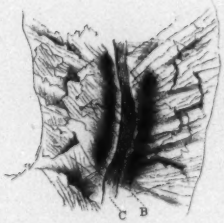


Fig. 12. × 250 diameters

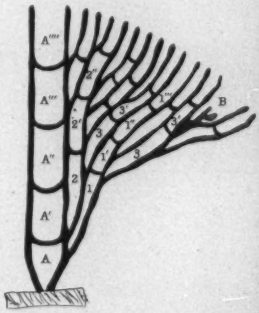


Fig. 15.

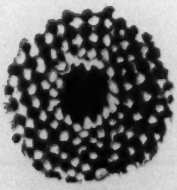
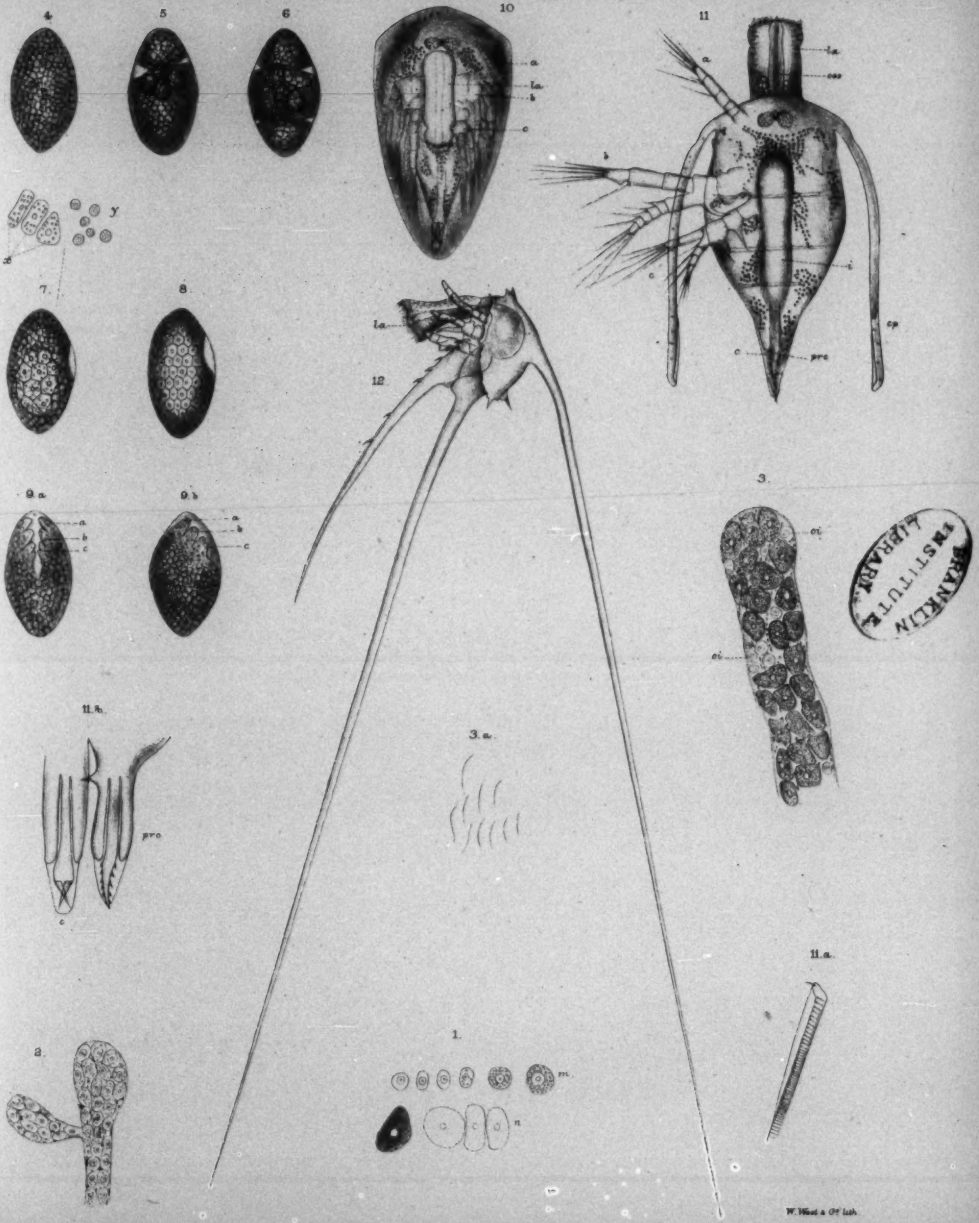


Fig. 17. × 10

Fig. 14. × 80 diameters



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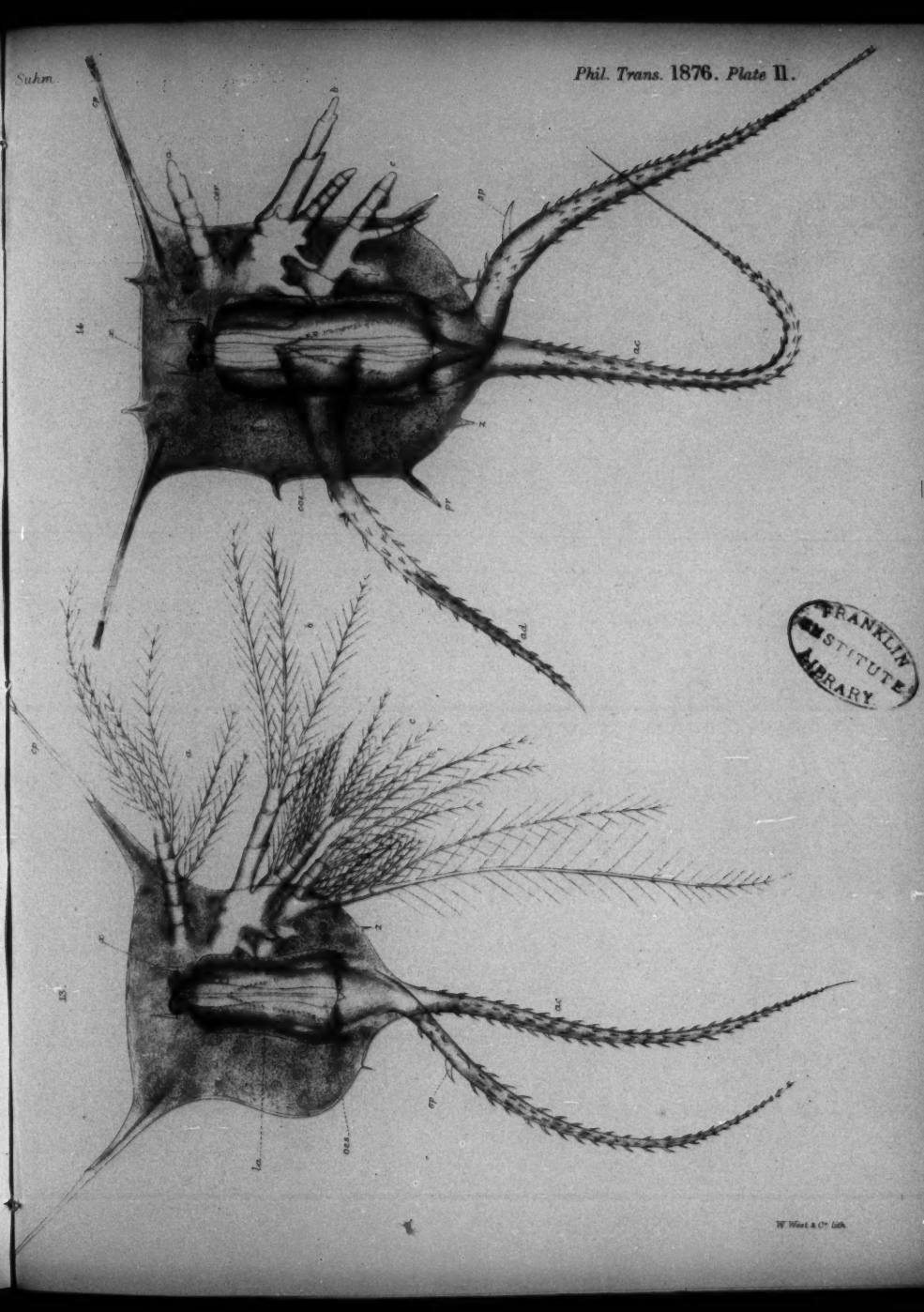
Phil. Trans. 1876. *Plate* II.



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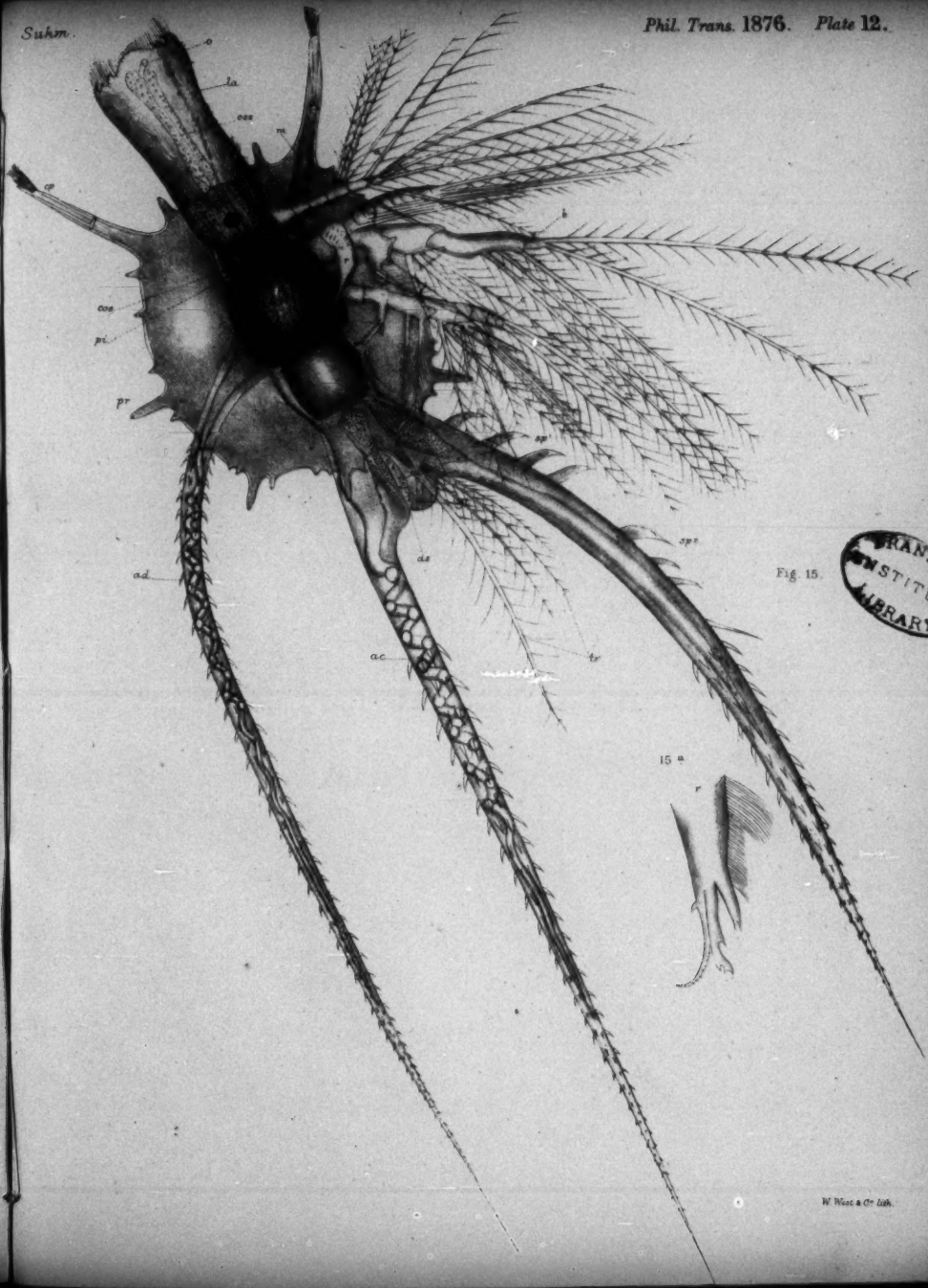

Fig. 15.

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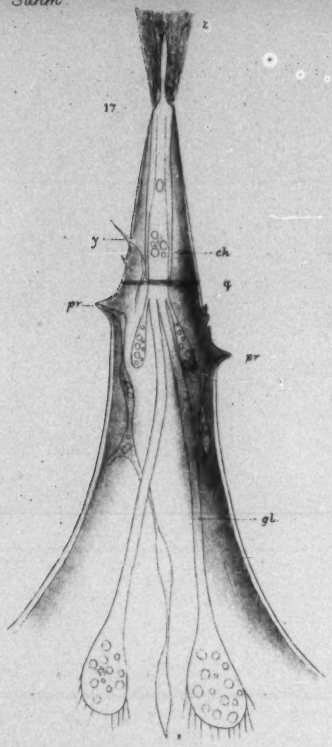

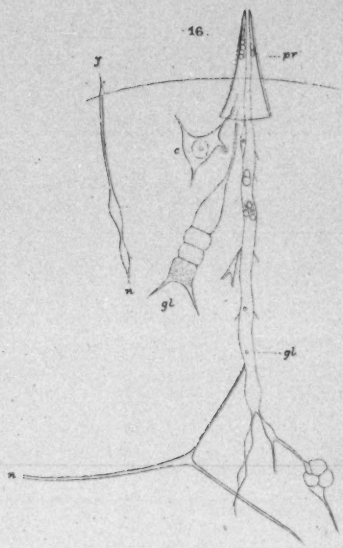

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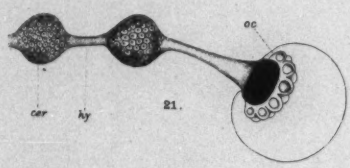

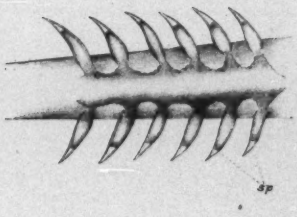

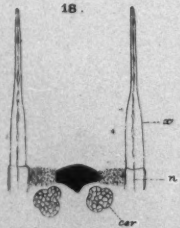

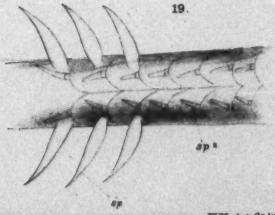

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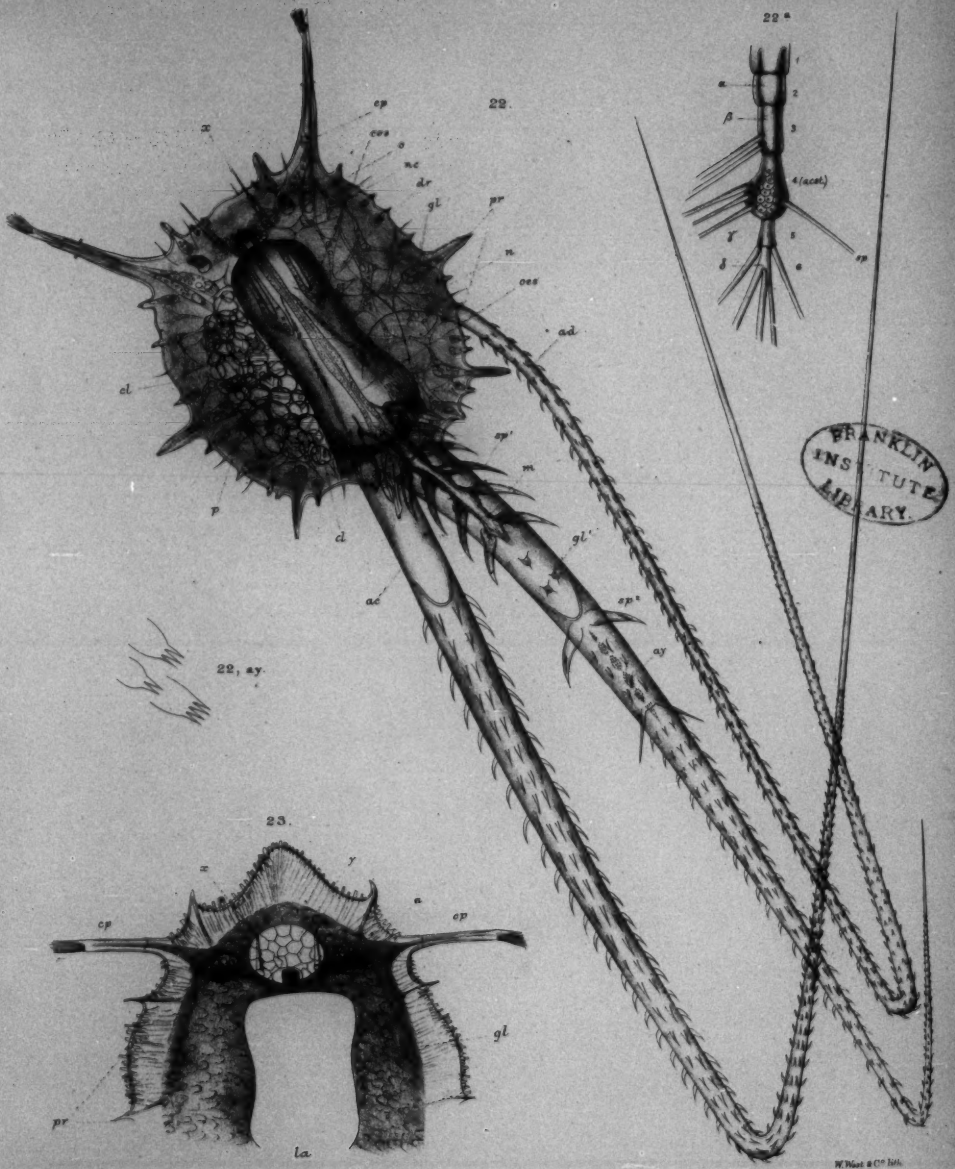

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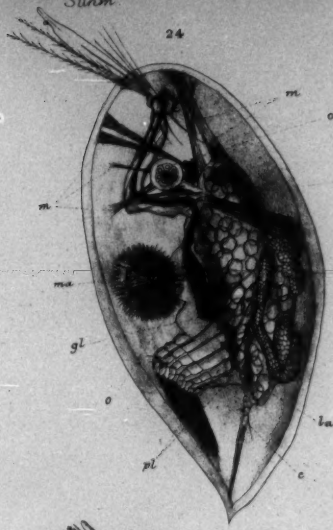

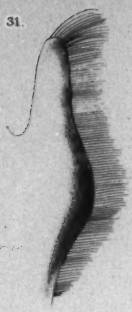

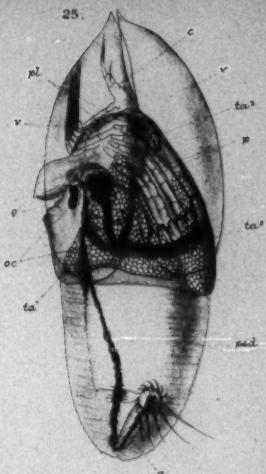

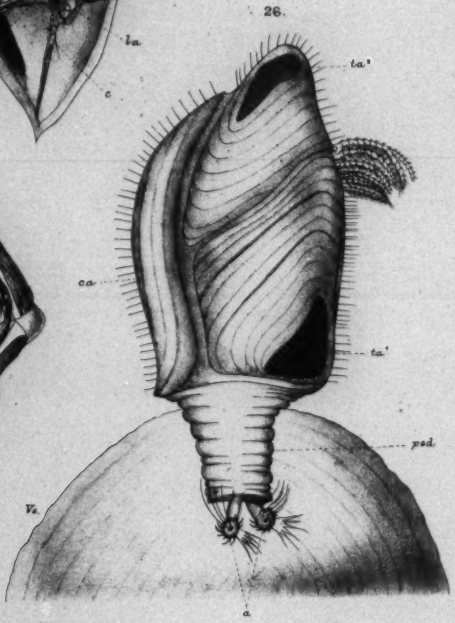

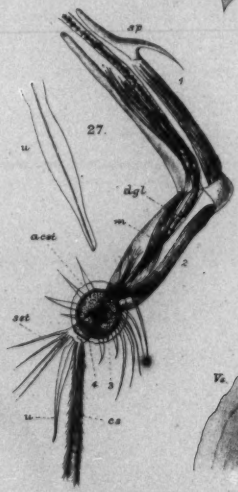

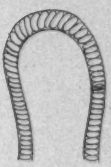

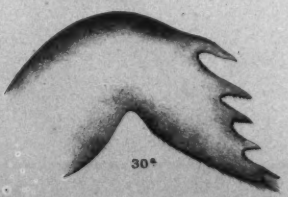

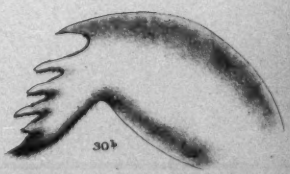

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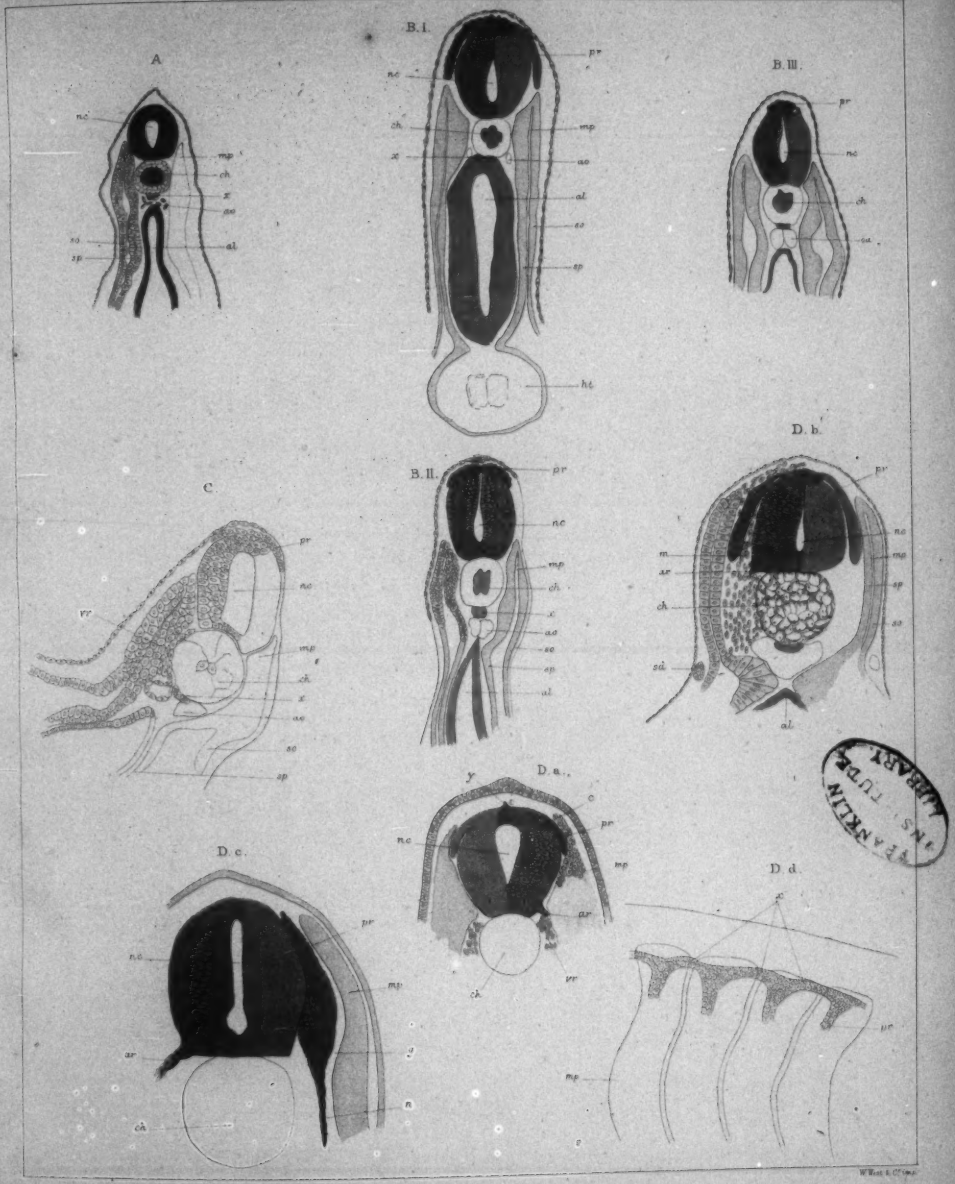
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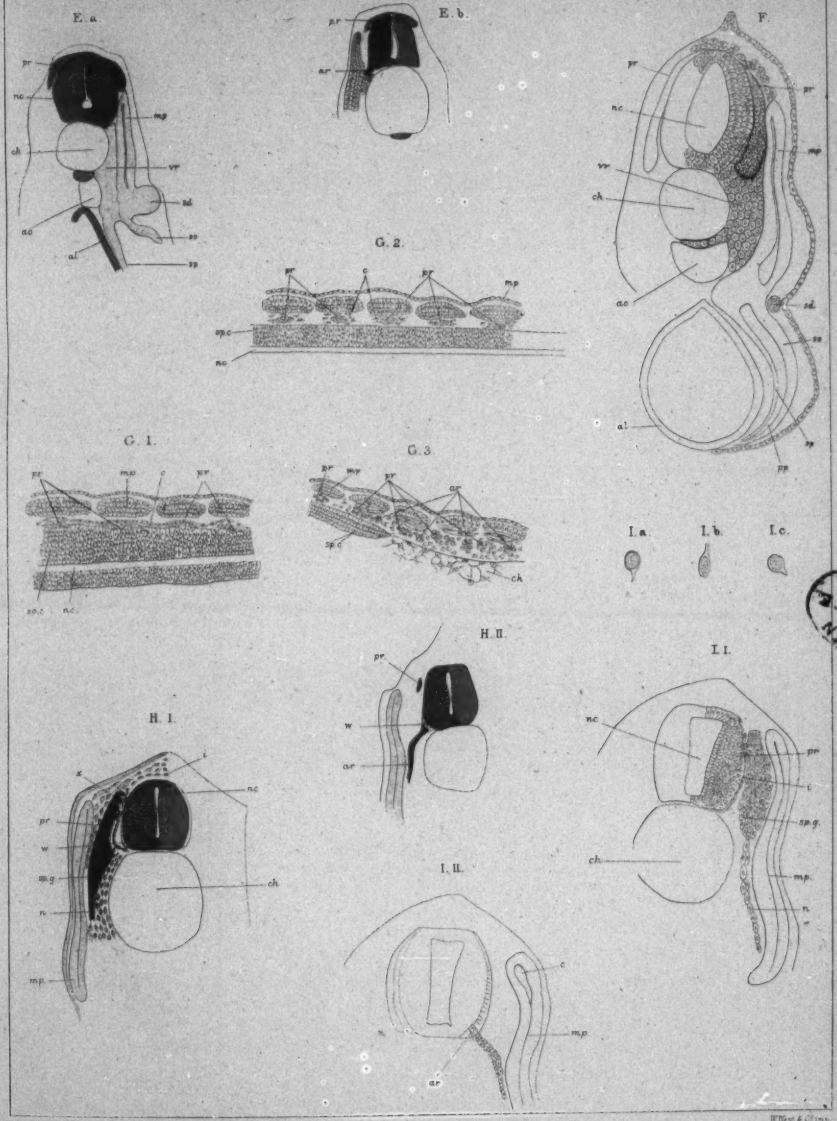

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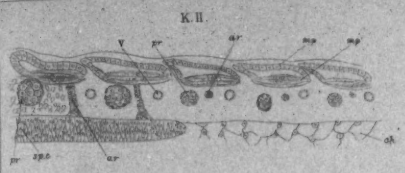

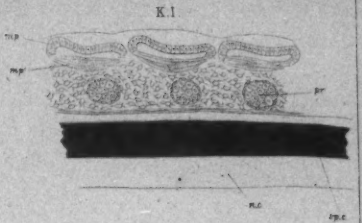

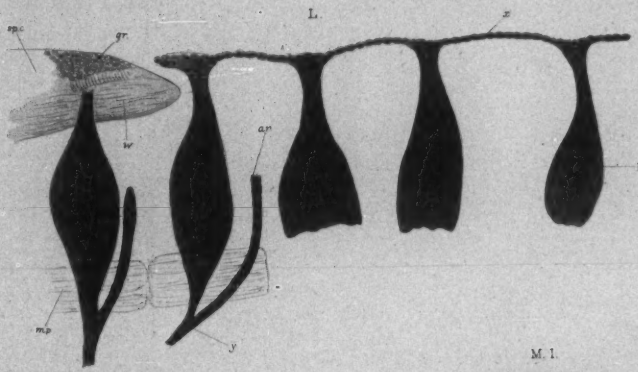

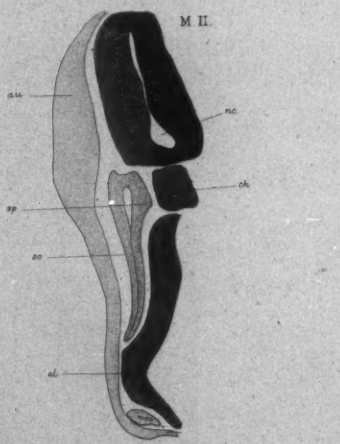

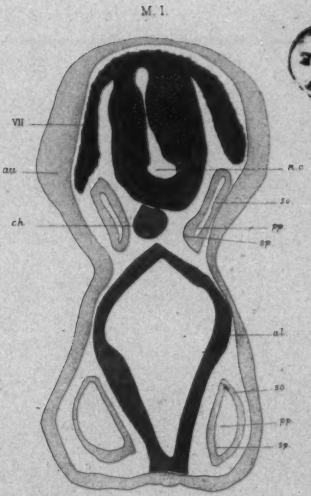

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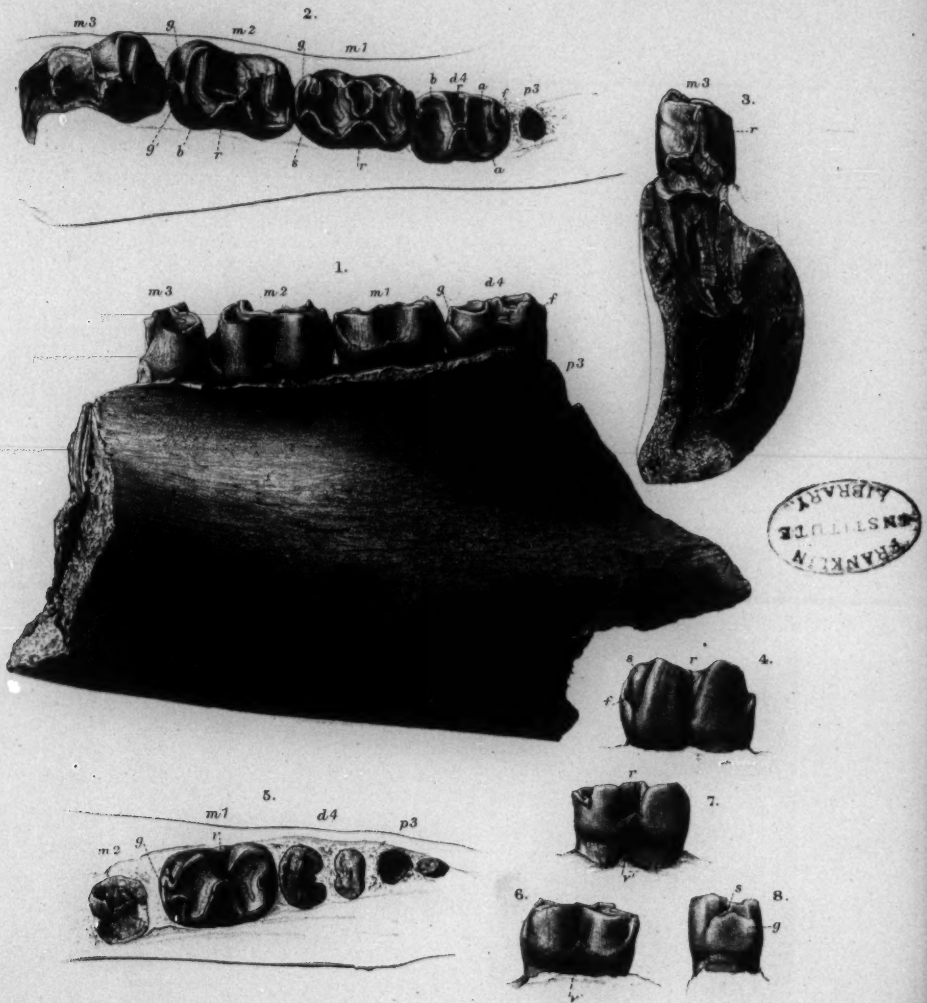

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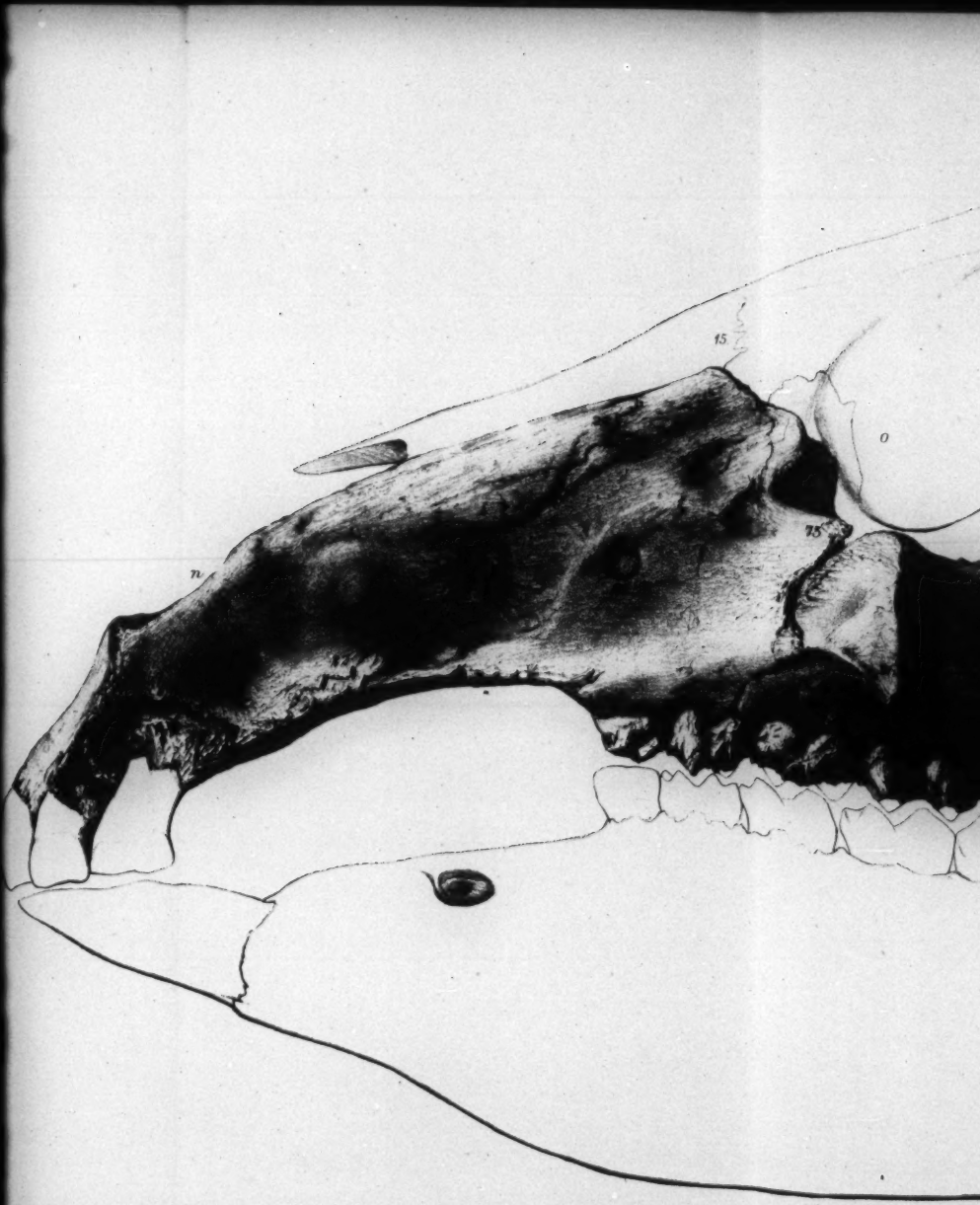
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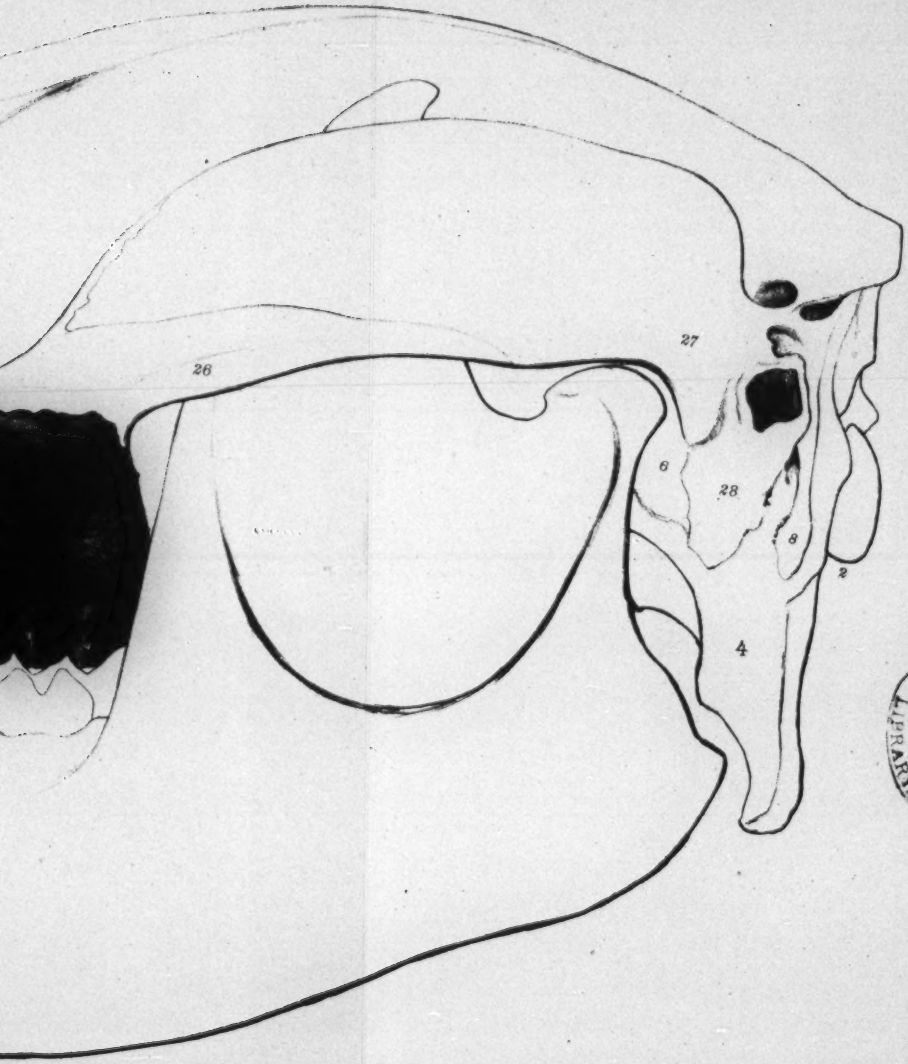

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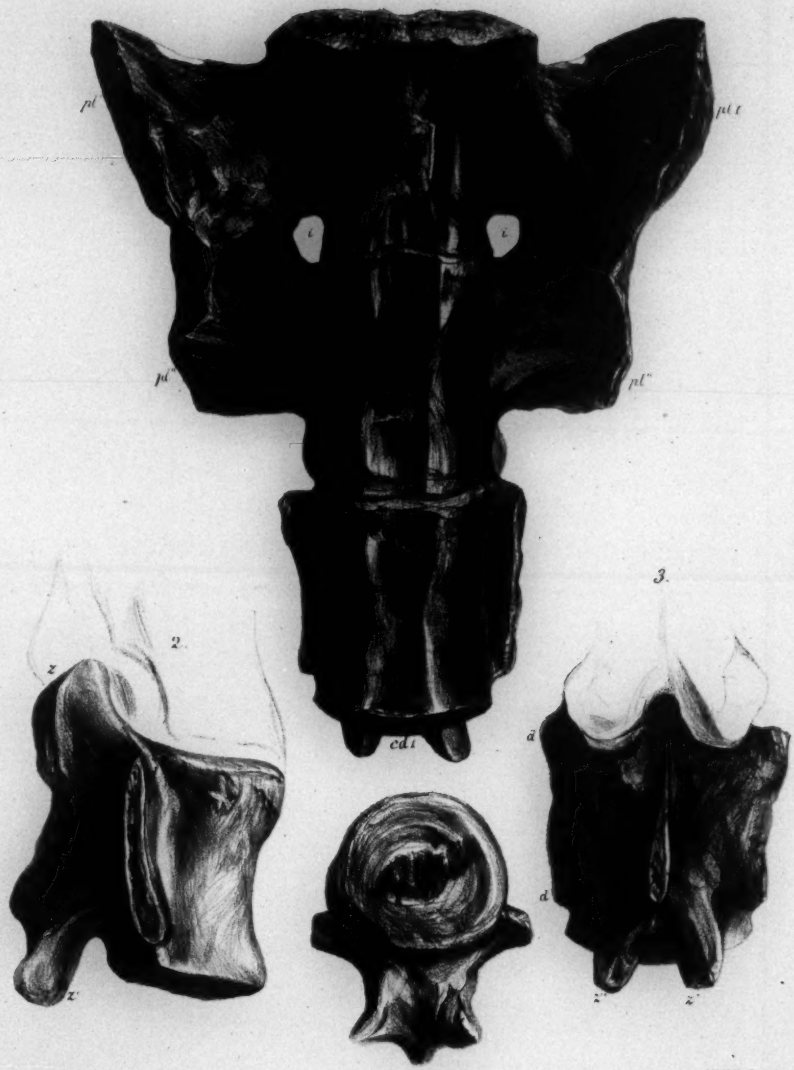

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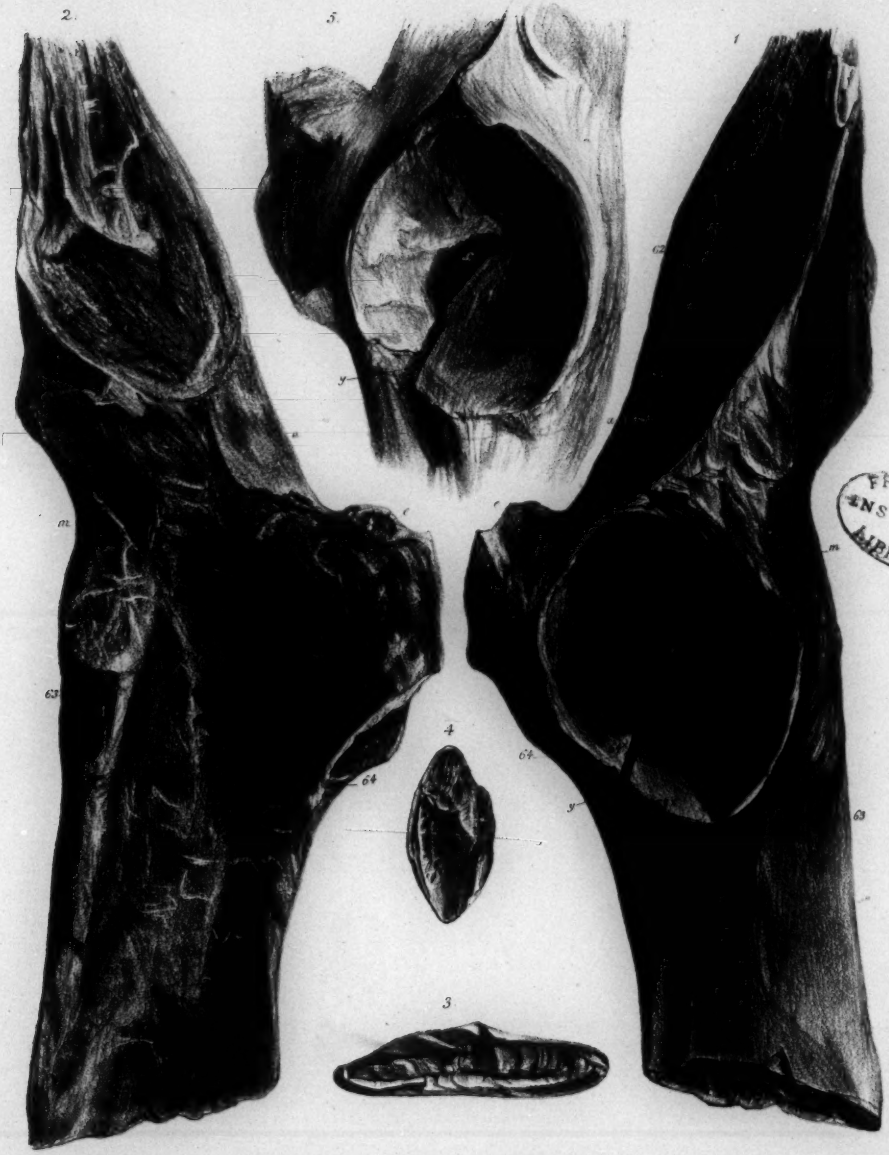

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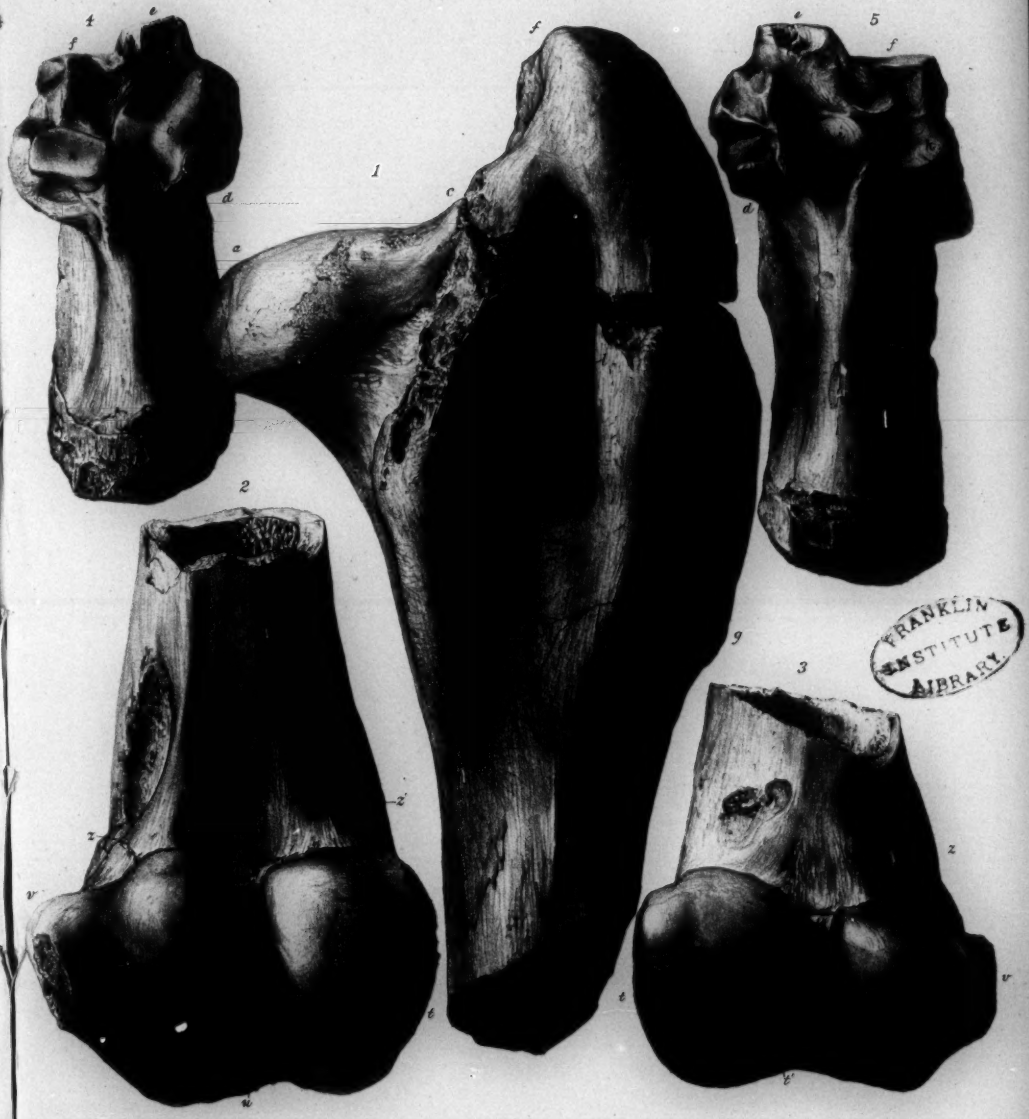

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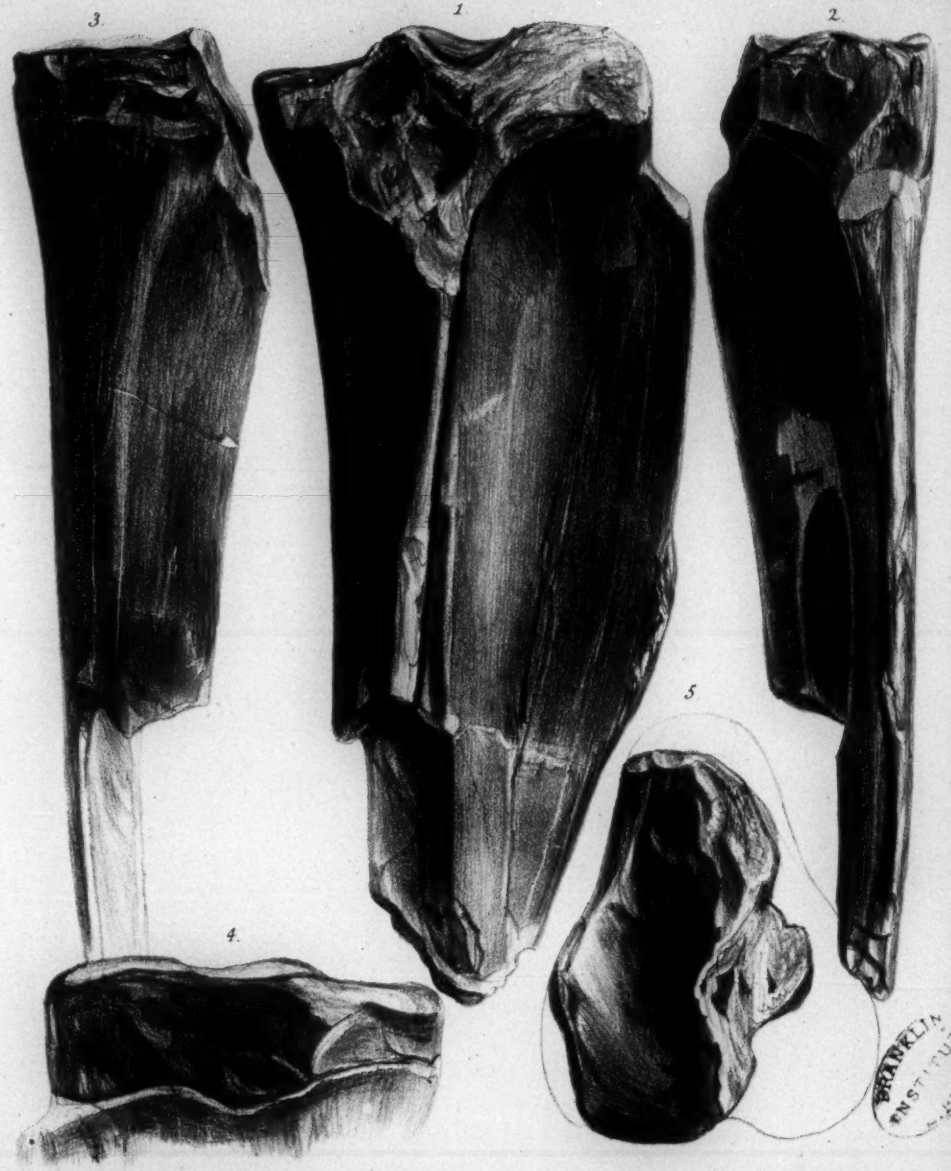

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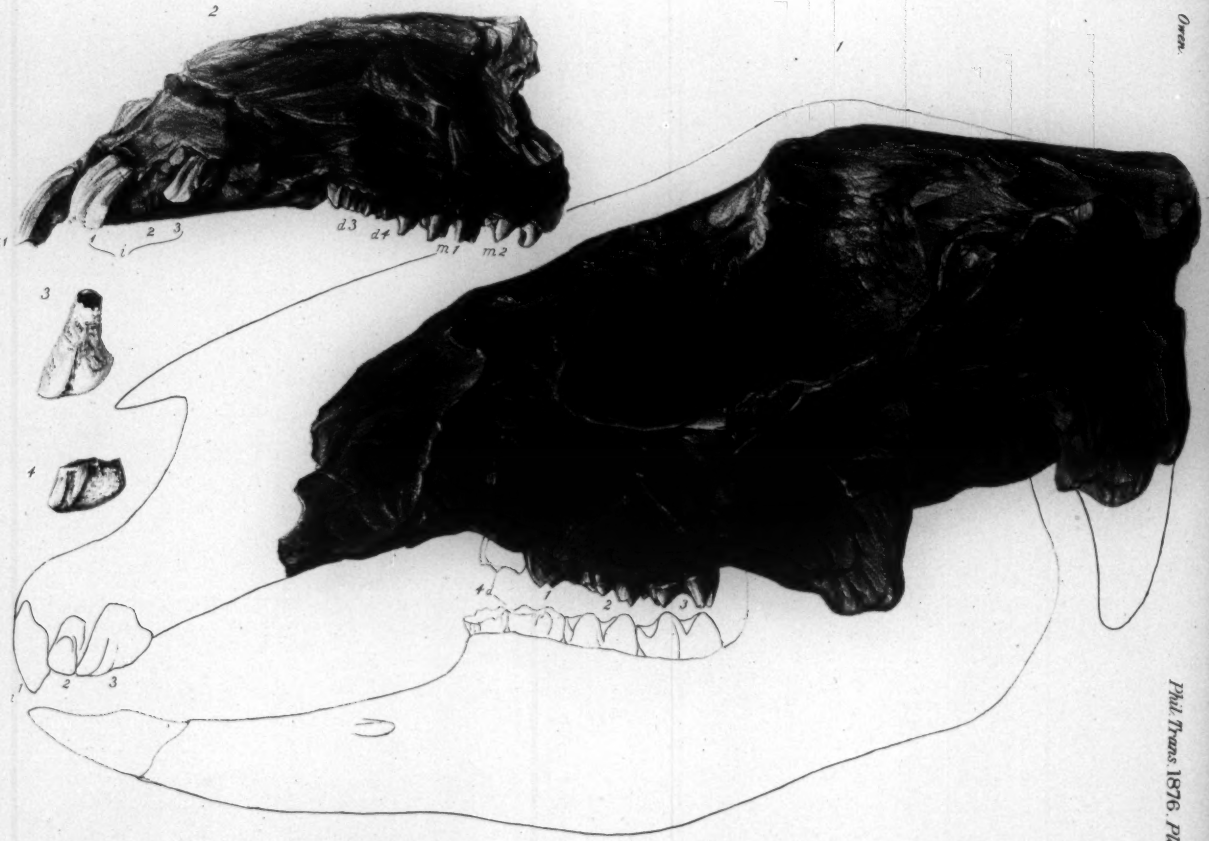

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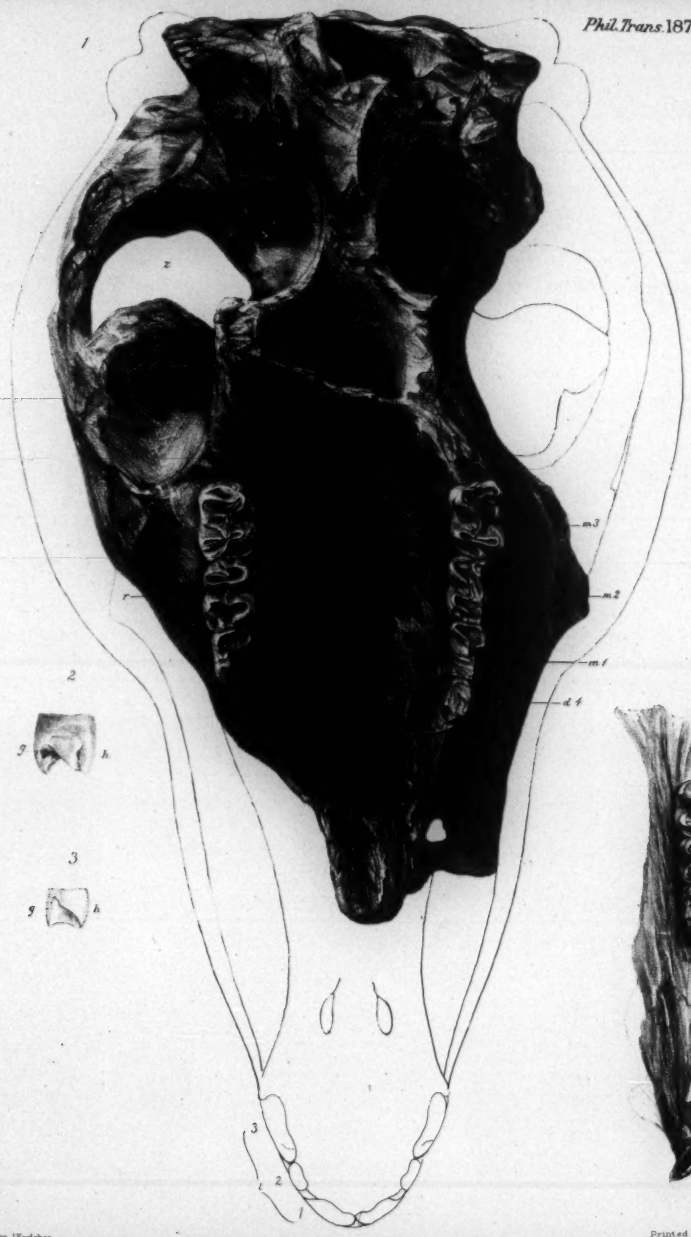

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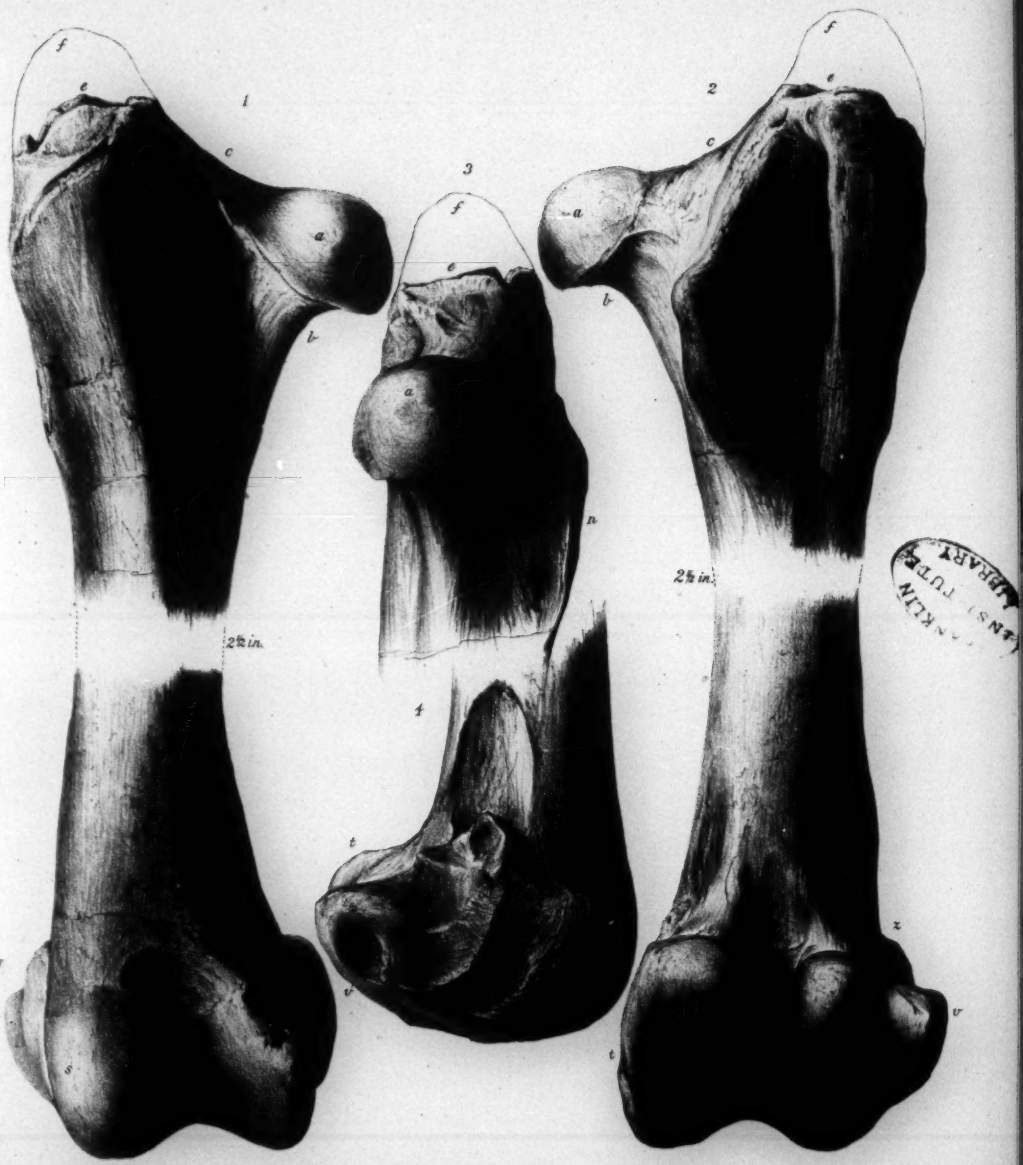

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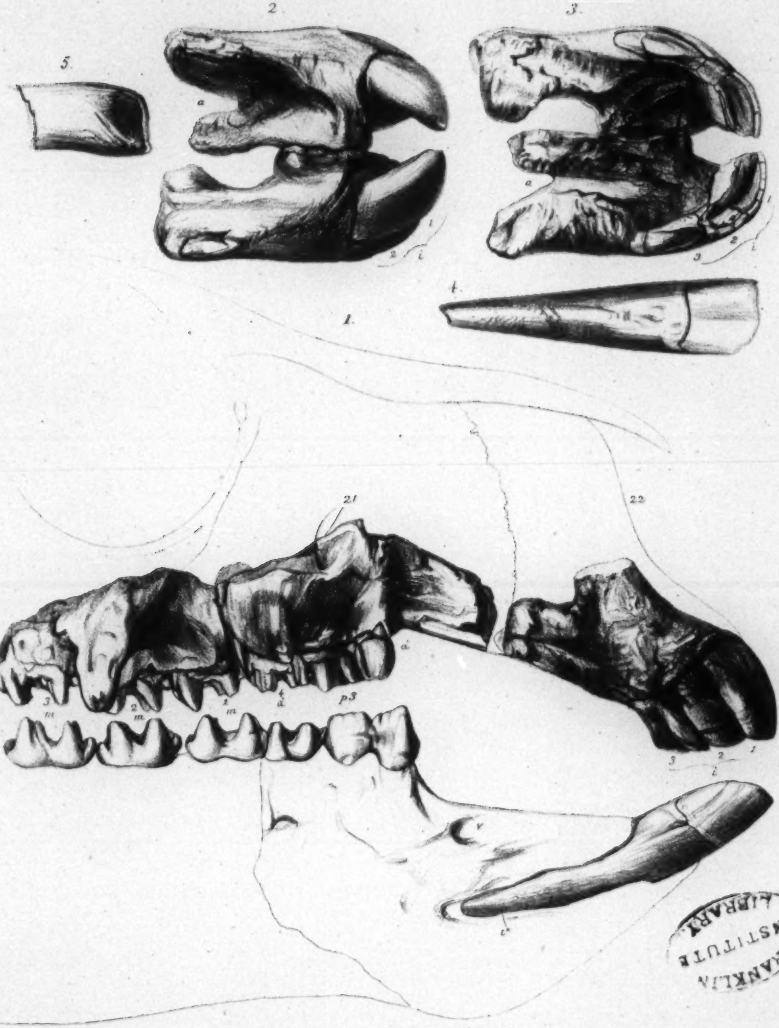

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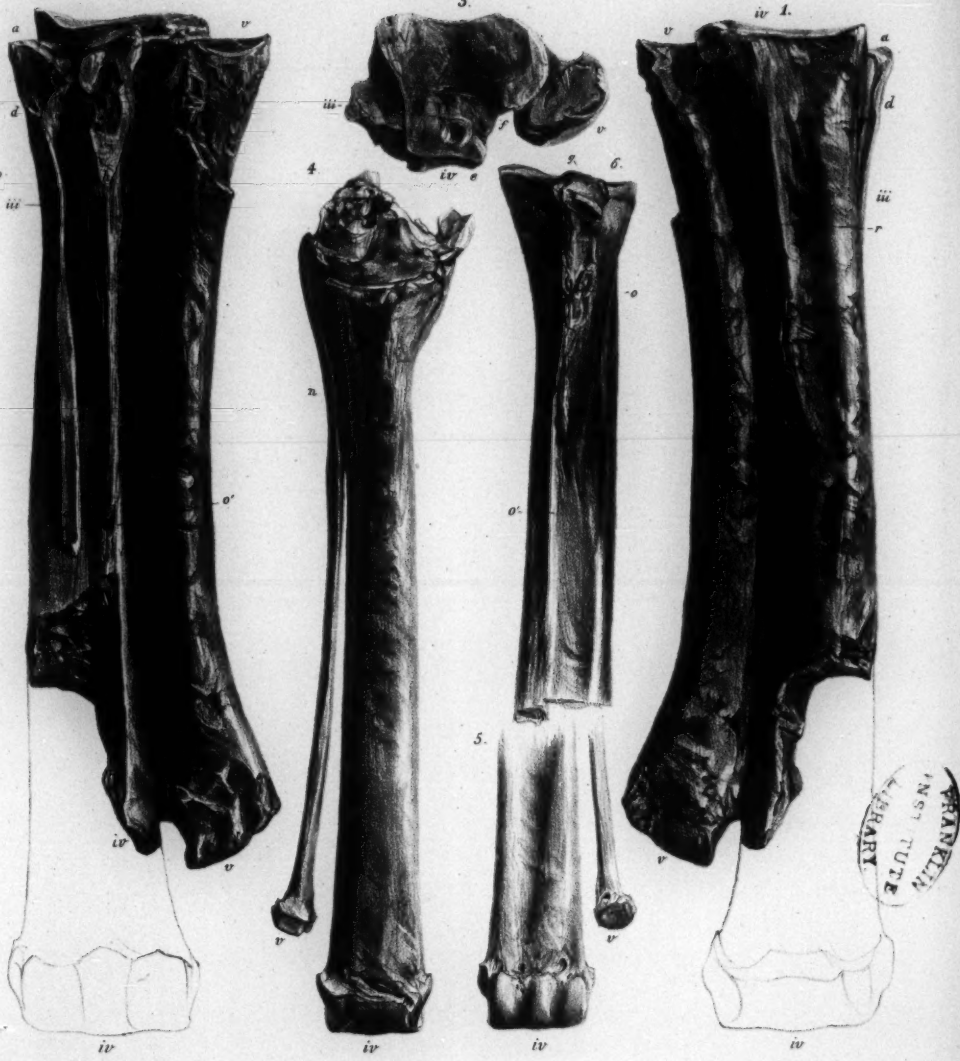

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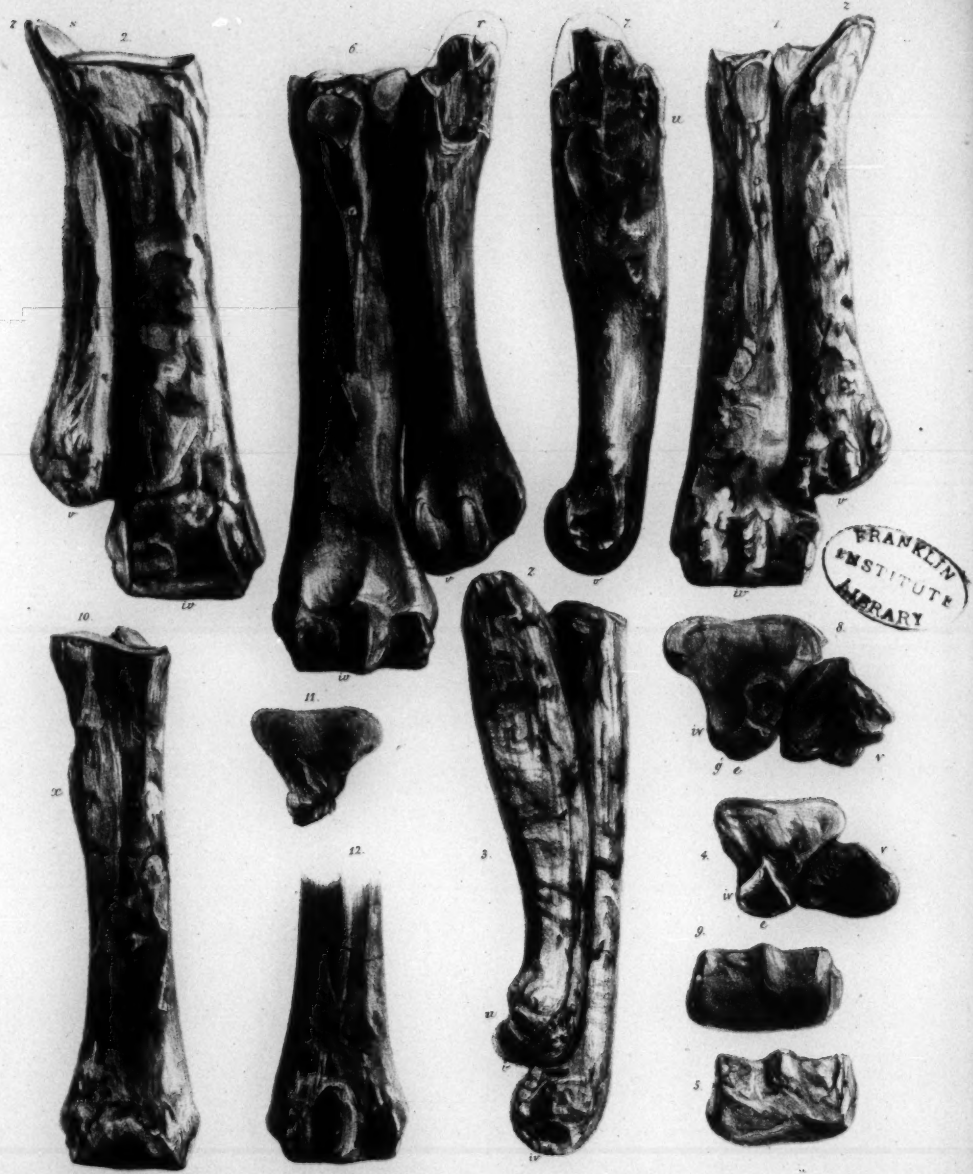

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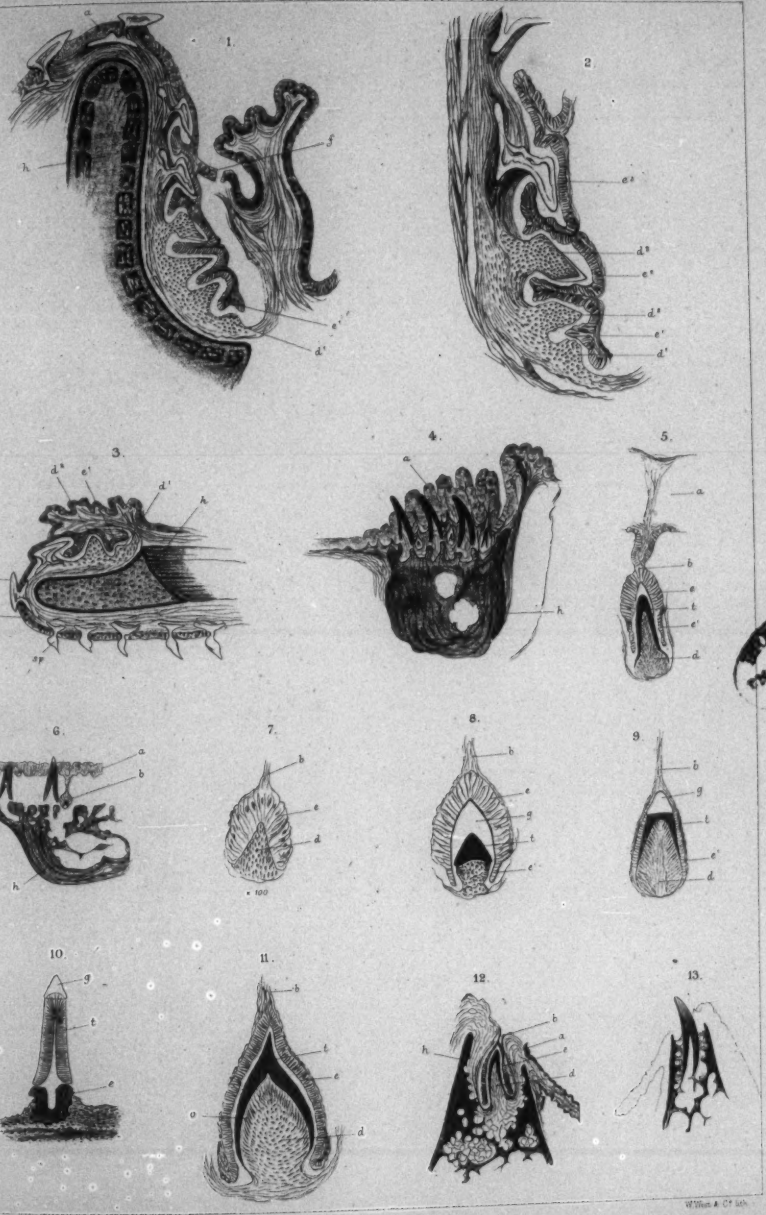

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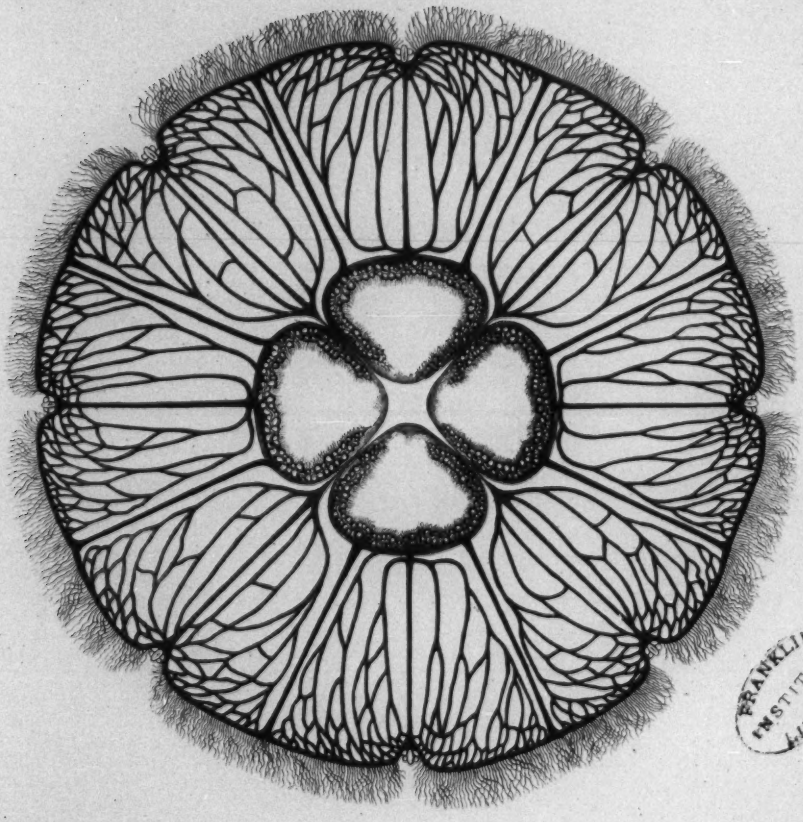

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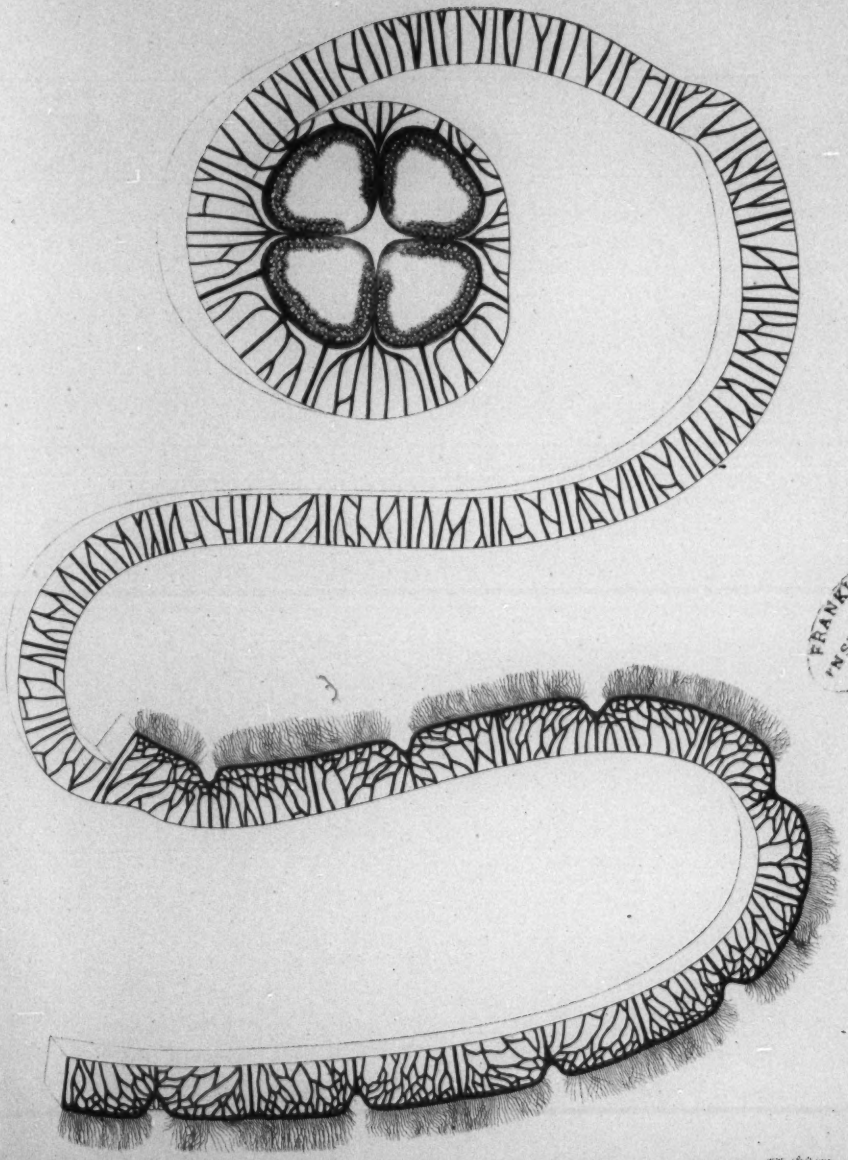

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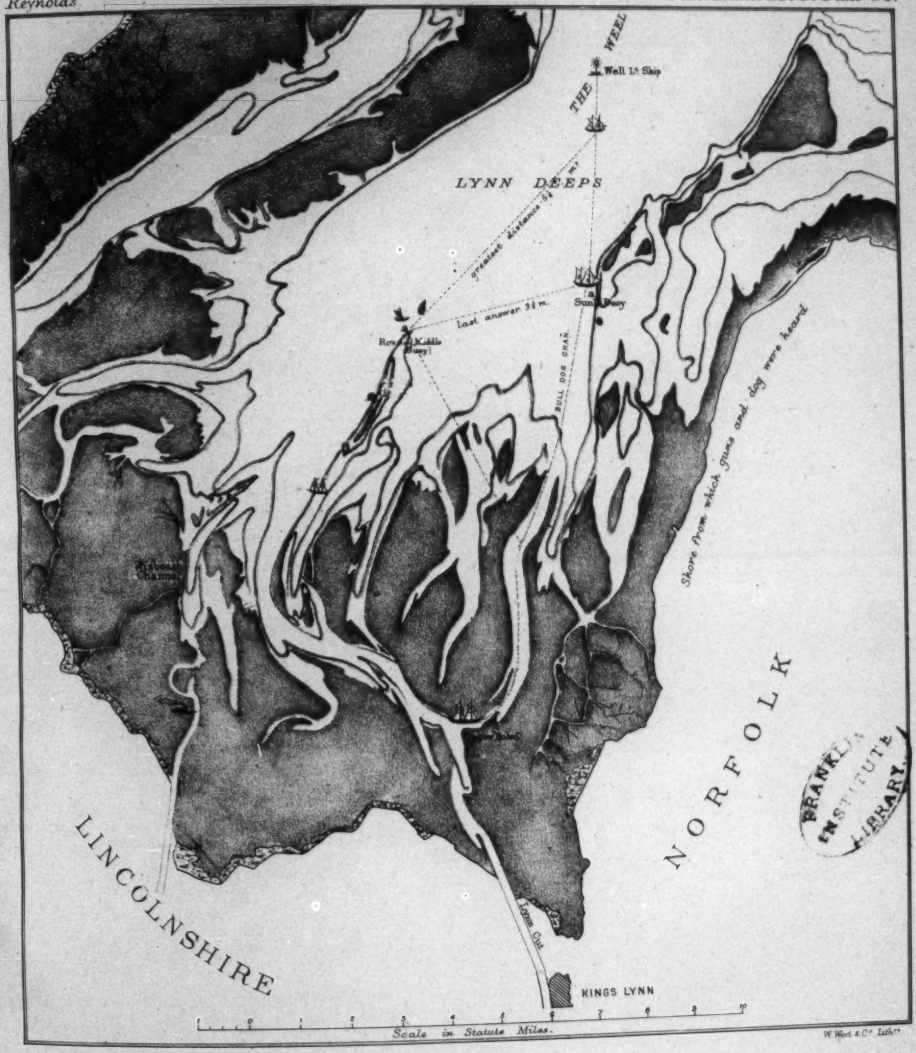

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